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THE CONCEPT OF ECOSPECIES IN TERTIARY PALEOBOTANY

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In his studies of Tertiary floras in the western United States, the paleobotanist has been able in most cases to apply an ecological approach to problems of past environment with a reasonable degree of accuracy.[1,3,12–20] This has been due to the fact that middle and later Tertiary floras, although subjected to considerable later Cenozoic segregation, still resemble living units of vegetation. Data for paleoecological interpretations of the Miocene forest which occupied the Columbia Plateau and northern Great Basin are assembled from the modern Redwood, Coast and Sierra-Cascade forests of the Pacific states, from the hardwood-deciduous and coniferous forests of eastern North America and eastern Asia and from the temperate highlands of central and southern Mexico. In the case of Miocene floras from southern California reconstructions are based on woodland, chaparral, desert-scrub and thorn-forest communities now living in southern California, the southwestern United States and northern Mexico.[3] A synthesis of the environmental conditions suggested by the various elements provides a general index to conditions existing at the time a fossil flora was deposited.

But in certain floras, and particularly in those of later Tertiary age, there may be mixtures of plants from habitats so widely different that explanation is difficult. In the Sonoma flora north of San Francisco Bay,[9] for example, members of a humid coast forest, including such species as *Abies* (*grandis*),† *Rhododendron* (*californicum*), *Sequoia* (*sempervirens*), *Tsuga* (*heterophylla*) and *Vaccinium* (*parviflorum*), lived at no great distance from such semi-arid plants as *Quercus* (*engelmannii, tomentella, douglasii*), *Platanus* (*racemosa*) and *Ilex* (*brandegaena*). A comparable mixture occurs also in the Remington Hill flora from the central Sierra Nevada,[22] where the mesic *Sequoia* (*sempervirens*) and *Chamaecyparis* (*lawsoniana*) are found with *Mahonia* (*haematocarpa*) and *Ungnadia* (*speciosa*), which are now typical of semi-arid and even desert-border habitats

in the southwestern United States. And in the Alvord Creek flora of southeastern Oregon,[11] high montane species of *Abies* (*shastensis*), *Sorbus* (*californica*), *Picea* (*engelmannii*) and *Pinus* (*murrayana*) lived at no great distance from such chaparral species as *Ceanothus* (*cuneatus*), *Cercocarpus* (*betuloides*) and *Photinia* (*arbutifolia*), which occur today fully 3000 feet below the zone where the montane species survive.

These and similar instances have been explained on the basis of the overlap of the Sierra Madrean element on the mesic northern forest.[2,3,9,10,11,22] It is now known that as the climate became drier and warmer at middle latitudes in the late Miocene and early Pliocene, the Sierra Madrean element, to which these species of *Ceanothus*, *Cercocarpus*, *Ilex*, *Mahonia*, *Quercus* and *Ungnadia* belong, migrated northward and overlapped the northern forest which at this time was restricted largely to compensatory sites in areas of low to moderate relief. Another factor which accounts for these peculiar assemblages is the fact that Miocene and Pliocene vegetation had a generalized composition. The modern coniferous and woodland associations in the western United States were derived from the Miocene and Pliocene forests by climatic segregation only in the late Cenozoic.[4,7,26]

It is evident that the occurrence of ecospecies[21,28] in the fossil record might afford still another explanation of some of the peculiar habitats apparently occupied by certain fossil species closely related to living plants. This concept has been brought to attention mostly by the fact that Miocene and Pliocene species closely related to modern endemics of narrow ecological limits apparently lived under diverse climates and with widely different types of vegetation in middle and later Tertiary times. Two of the more notable examples which are provided by *Sequoia* and *Lyonothamnus* may be briefly reviewed.

The Tertiary distribution of *Sequoia langsdorfii* in the northern hemisphere illustrates the diverse conditions under which certain fossils related to modern endemics were able to survive. The coast redwood, *S. sempervirens*, which has generally been considered as most nearly related to *S. langsdorfii*, now lives in the coastal fog belt from southwestern Oregon southward for 400 miles into the Santa Lucia Mountains of central California. Yet in the Eocene *S. langsdorfii* has been recorded in Grinnell Land at 83° N. latitude, in a region where there are now several months of comparative darkness, with such typically boreal types as alder, spruce and willow.[24] On the southwestern coast of Alaska the Eocene associates of *S. langsdorfii* included warm-temperate species of palm, cycad, laurel and other low-latitude genera, in addition to typically temperate genera.[25] The composition of the forest at middle latitudes in the Miocene depends largely on position with respect to the ocean. In the coastal region of Oregon it has been recorded with relicts of the Eocene forest which were surviving at this time in favorable coastal valleys,[17] but at the interior its

associates are largely temperate genera. In later Tertiary time, members of the Sierra Madrean woodland-chaparral element lived on exposed slopes bordering *S. langsdorfii;* examples are provided by the Sonoma,[9] Remington Hill[22] and Idaho floras.[23]

Lyonothamnus, a monotypic member of the Rosaceae which is now limited to the Channel Islands off the coast of southern California, has been discovered at a number of Miocene and Pliocene localities in California. In the Miocene of interior southern California,[3,5,6] it has been recorded with woodland, chaparral and desert-border vegetation whose nearest equivalents now survive in California, the southwestern United States and northern Mexico. Also represented in these floras are members of a sub-tropical thorn-forest (*Bursera, Colubrina, Dodonaea, Euphorbia, Ficus, Pithecolobium, Randia*) which now lives on the west coast of Mexico from central Sonora southward. In the Upper Miocene Puente flora of coastal southern California, *Lyonothamnus* is recorded together with members of an oak community whose nearest derivatives now occur in Mexico, and with relicts of the Eocene (*Anona, Magnolia, Ocotea, Sabal*) forest which were surviving near the coast at this later date. In the Middle Pliocene Mulholland flora of the San Francisco Bay region,[7] *Lyonothamnus* lived in proximity to members of a border redwood forest (*Amelanchier, Arbutus, Corylus, Fraxinus, Populus, Prunus*), relict members of the East Asian and East North American elements (*Berchemia, Nyssa, Populus, Quercus*), and trees and shrubs whose nearest equivalents now survive in the Rocky Mountains.

In addition to these examples provided by *Lyonothamnus* and *Sequoia*, it must be added that fossil species related to such modern endemics as *Ginkgo biloba, Glyptostrobus pensilis, Picea breweriana* and *Quercus tomentella* also had fully comparable occurrences during Tertiary time.

A remarkable example of the diverse habitats occupied by a later Tertiary non-endemic is the occurrence of *Populus pliotremuloides* Axelrod. The leaves of this aspen are indistinguishable from those produced by the living *P. tremuloides* in the drier portions of its range in the western United States. Where it occurs with montane vegetation in the fossil record its interpretation is obvious, for aspen still occurs with upland forests over a large part of its range. But in the Miocene and Pliocene of southern California,[1,3] aspen has been recorded with desert-border vegetation as well as with members of a sub-tropical thorn-forest which now survives on the west coast of Mexico in an area where frosts are essentially absent. In the Pliocene Oakdale flora of the lower central Sierra Nevada foothills,[8] it lived along streams in a region dominated by oaks whose nearest equivalents are *Quercus douglasii* and *Q. wislizenii*. And in the Sonoma flora near Santa Rosa,[9] it is recorded with coast redwood and members of the Coast Forest. Significantly, its larger-leafed Miocene counterpart, *P. lindgreni*, was a

regular associate of the Miocene redwood forest in the Columbia Plateau and northern Great Basin. This species differs from *P. pliotremuloides* in that its leaves are more nearly like those found on aspen today in mesic rather than in semi-arid portions of its distribution.[18] It seems obvious that when they are compared with the living *P. tremuloides*, both *P. pliotremuloides* and *P. lindgreni* must be recognized as ecotypes which are no longer living, for nowhere in its range today does aspen approach thorn-forest, oak woodland or redwood forest. Nevertheless, aspen still is one of the most diversely distributed trees in North America today. And in this distribution, which extends from Alaska southward into Mexico, and from the Pacific to the Atlantic, it grows under widely different conditions. It seems highly probable that the living species may also be represented by more than one ecotype over this wide area.

Such occurrences readily illustrate the fact that fossil plants related to modern endemics, and other species as well, lived under diverse climates and with widely different types of vegetation in Miocene and Pliocene times. They lend considerable support to the belief that it is possible for a species to cross widely different climatic areas only at a time when its number of biotypes and range of tolerance are greatest. And in the cases noted above, this seems to have been in the Tertiary. Although there can be no question that many fossil plants closely resemble living species, it would appear that some of these which are related to modern endemics probably should be considered as ecospecies of considerable ecological plasticity, rather than related to species of narrow ecological limits. From this standpoint, such relict endemics as *Fremontia californica*, *Ginkgo biloba*, *Lyonothamnus floribundus*, *Glyptostrobus pensilis*, *Picea breweriana* and *Sequoia sempervirens* would represent survivors of more widely distributed ecospecies of greater ecological adaptabilities. It is significant in this connection that Stebbins has pointed out that *Fremontia*, *Lyonothamnus* and *Sequoia* are polyploids, and that they appear to be remnants of older and formerly more widespread species-complexes.[27] Obviously not all endemics are polyploids, but the relation of polyploidy to the broader aspects of evolution is apparent from the following statement by Stebbins[27]:

". . .the odds are against the polyploid complex as being the originator of any really new line of evolution. . . .It can produce endless new species, but these are all or nearly all new combinations of the same supply of genic material. . . .There are hundreds of species of *Rosa*, *Rubus*, *Potentilla*, *Senecio* and *Poa*. . .most of which have arisen by polyploidy. . . . With increasing age, the polyploids. . .begin to die out, so that in the last stages of its existence a polyploid complex is simple once more, and is a monotypic or ditypic genus without any close relatives. . . ."

Significantly, there is evidence of the existence of species-complexes related to modern insular endemics during the middle and later Tertiary.

In the case of *Lyonothamnus*, there are indications that more than one species may have been in existence during Miocene and Pliocene times. Records of *L. mohavensis* Axelrod from regions where it is associated with desert-border vegetation, as in the Tehachapi[3] and Mint Canyon floras,[5] are represented by leaves which are about one-half the size of those produced by the modern species. On the other hand, specimens from more coastal localities, as in the Puente and Mulholland floras,[7] are intermediate in size with respect to the interior *L. mohavensis* and the modern insular *L. floribundus*. It is apparent that these small- and intermediate-leafed forms may represent members of a polyploid complex which became extinct only in the late Cenozoic. This same general relationship has been noted also for another insular endemic, *Quercus tomentella*. Where its equivalent first appears in the record, which is also in the early Miocene of the western Mohave region,[3] the fossil leaves more nearly resemble the smaller ones produced by the living species. Yet in coastal Pliocene localities in central California,[7,9] they commonly are of intermediate size and often resemble the modern in all details. In this instance there is evidence also for the gradual elimination of smaller-leafed ecotypes from semi-arid interior regions, with an insular survival of a modern endemic having no close living relatives.

It is true that the paleobotanist may not always be able to distinguish these forms taxonomically from one another or from living plants, owing to the fragmentary nature of the material with which he is dealing. But from a distributional and ecological standpoint, the fact that the fossil representatives of many endemics bordered climates widely different from those in which their nearest relatives live, and were associated with plant communities now occurring in diverse geographic areas suggests that the concept of ecospecies may have an important place in interpreting middle and later Tertiary floras. It is well known that plants were forced to adjust rapidly to new environments in the later Cenozoic. At this time in western North America rainfall was being lowered, summer showers were disappearing, temperature ranges and extremes were increasing and greater topographic diversity was resulting from orogenic disturbances. Studies of later Tertiary floras during the past decade have served to emphasize the dynamic character of late Miocene and Pliocene environments. They clearly reveal wide restrictions of ranges of living derivative species, as well as climatic segregation of plant communities. And it must be emphasized that there are indications also of accompanying changes in physiological requirements of species. In certain instances ranges of tolerance apparently were extended so as to withstand harsher conditions; other plants show restriction from arid interior habitats to more moderate coastal and insular areas.[7]

In view of these facts, it seems highly probable that many Miocene and

Pliocene species related to living endemics may represent extinct ecotypes of more widely distributed Tertiary ecospecies. On this basis the modern endemics would, in some cases at least, be interpreted as surviving under conditions somewhat different from those occupied by their nearest related fossils. In other words, fossil representatives of endemics and other species occurring in habitats widely different from those now occupied by their closest descendants probably represent ecotypes having no close counterpart in the modern flora. The concept of biotype depauperization has been discussed largely by botanists concerned with the problem of boreal and alpine floras, but it apparently had an even more important rôle in later Tertiary time, with the rapid development of diversified climate, topography and vegetation.

Conclusion.—The Tertiary distribution of the fossil equivalents of modern endemic trees and shrubs brought them into contact with diverse types of climate, habitat and vegetation. Available evidence suggests that when fossil species related to these endemics are recorded in habitats which are widely different from those now occupied by their nearest descendants, we may be dealing with ecotypes having no close counterparts in the modern flora. Late Cenozoic elimination of biotypes apparently has left the modern endemics surviving in habitats which may be considerably different from those occupied by certain of their close fossil relatives; a similar interpretation may be applied also to certain other trees and shrubs.

Since paleoecological interpretations are based on plant communities, and not solely on individual species, the recognition of ecotypes in the fossil record has no effect on the general procedure for reconstruction of past environments. On the contrary, their recognition makes it possible to explain certain inconsistencies of association which otherwise defy interpretation.

* A contribution to the later Tertiary paleobotany of the western United States which was largely completed during tenure as National Research Council Fellow at the U. S. National Museum, 1939–1940 and 1940–1941.

† Species in parentheses throughout this report represent close living equivalents of fossil species.

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PATTERNS OF GROWTH IN HUMAN INTELLIGENCE

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What we seek in the measurement of intelligence is the capacity of any person to acquire knowledge, to see relationships and to solve problems. The mental tester, whatever his theoretical position, faces the practical necessity of measurement in terms of verbal instruction. His test items are highly saturated with differential experience and education.

In the twentieth century, a population is likely to be heterogeneous with respect to race, family background and education. The organic differences that are present long before birth cannot be isolated by a social device. These differences do not stem from a single source, but vary from the predominantly innate to the predominantly accidental or learned. The growing fabric of intelligence is a product of the organism's total experience. Because of certain combinations of limiting factors, there are some things the organism cannot become, but there is nothing that it must become.

In order to distinguish intelligence from achievement, mental tests are often said to measure original capacity. But one sure thing about mental ability is that it grows; this being true, the word "original" becomes anoma-

lous. One might ask, original at what time in the life history of the individual?

It is generally held that older persons work with less speed than younger. Since many group tests are timed, adults are handicapped. Even if a test is not timed, any failure to bring factors and conditions into juxtaposition rapidly may reduce performance. Here we enter a no-man's land with respect to the meaning of intelligence. External factors of speed may be ruled out of the definition if we so desire, giving every person ample time to show his mental power. But the internal factor of speed is another matter, for under certain conditions there is a genuine relationship between speed and power. Economy in the intellectual process means that false leads will be rejected early, that data and methods leading to the solution of an abstract problem can be mastered before dimness or stereotypy sets in. To take too long for a solution, is to endanger one's arrival at the goal.

From a large amount of research over the past two decades, it is clear that the intellectual standing of any person from infancy upward will be related to the pressures and opportunities in his cultural environment. What these effects are, involving what particular mental functions, in combination with what genetic factors—all this is a long, complicated story which cannot be reviewed here. But it has bearing upon the pattern of growth that may be expected in later life. A wide shifting in IQ among children, together with a tendency of the IQ to rise in relation to good environment and to fall with cultural deterioration, has been established. For example, the general tendency of foster children to reach an average or above-average status under good social conditions, regardless of the measured or imputed quality of the true parents, is no longer a matter of controversy. In Iowa, year after year, we add to the sampling of several hundred illegitimate children from the lowest social levels who, placed early in good adoptive homes, reach at the preschool and school ages, a level of intelligence well above the mean of the American population.

The most extensive data in the Thirty-Ninth Yearbook of the National Society for the Study of Education yield an estimate of a shift of 20 IQ points or more in 16 per cent of grade school children. Such shifts involve changes up to 50 IQ points, a maximum capable of carrying a school child from brightness to dullness, or vice versa. In research centers from California to New York, similar radical shifts in intellectual status have been reported. But more germane to our present discussion is this question: given two IQ's differing, let us say by 20 points, which one will be maintained over the years?

At the present time, postulate and minor evidence point to the last obtained IQ, whatever it may be, as the best estimate of future status. The concept of intelligence is analogous to determinations of physical ability

or health. If you want to know how fast a sixty-year-old can run or how far he can jump, it is better to disregard any records hung up in the days of turtle-neck sweaters; if you want a measure of health, it is better to subject him now to laboratory, clinical and behavior tests than to recall what a strong constitution he was born with, or how his great-grandfather survived the rigors of Valley Forge.

Even this distinguished group of academicians, desirous of getting a valid estimate of the quality of its sons and daughters, may well lay aside the proud books of lineage or parental achievement in favor of tests of mental aptitude, in conjunction with the marks obtained in standard subject matter from grade school to graduate college. In principle and in fact a set of such measures, however crude, will be more accurate than estimates that cut across the somewhat unbridgeable gap between parent and offspring.

Whatever the exact form of the mental growth curve, its later stages are marked by a decline, a decline that dips into senescence if the organism survives. But a cessation of mental growth may occur at almost any age. No generalized growth curve can describe the pattern for a single individual. Some children (the idiots) grow scarcely at all; as full-grown organisms they resemble neither man nor child, but something less than either. Other children grow with such relative rapidity that they may be designated "gifted." This means simply that in standardized mental tests they rank in the upper p per cent of a distribution of like-age children. In the early days of American testing this point was placed at IQ 140. For several decades there was a tendency to designate IQ's above 140 as indicative of genius. Enthusiasm over this has been dampened considerably by the discovery that such a rating may be reached by the upper fourth of all our college graduates. The scientific worker now agrees with the man in the street that being a genius was too easy! The tendency now is to lay the entrance requirement for genius at 170, but this does not help much in view of test inadequacies: "Binet testing offers little opportunity to show what new solutions or original patterns a child can produce. . . [it is] restricted to the simple, the piece-meal, the common, the overlearned."

To characterize the defective or deteriorated thinking of very old persons as "childish," is libelous to both child and man: the essential charm of the inquisitive child is lost, while the adult reactions thus sampled scarcely touch the fine qualities of character, judgment and geniality that are independent of recurrent forgetfulness.

We do get a convergence of child and adult responses in areas that have been allowed to lie fallow, as in graphic representation. To quote Professor Norman Cameron ("Functional Immaturity in the Symbolization of Scientifically Trained Adults," *J. Psychol.*, **6**, 161–175 (1938)):

". . . .our scientifically-trained adults, when they fall back upon a mode of symbolization abandoned in childhood, make use of it with a logical structure that is correspondingly immature. Such drawing, in the average adult, represents a functionally immature form of symbolization coexisting at least potentially with the socially mature forms. . . .Entirely apart from emotional distortions and repressions, one finds in the symbolization of the mature adult, side-by-side, systems that differ widely in relative maturity. This fact alone invalidates assumptions that aim at setting up childhood thinking as something entirely distinct from the thought of the adult" (p. 172).

There have been a few attempts to measure abnormal forms of adult deterioration. In general, psychotics become slower and stickier in their mental reactions. They tend intellectually to get out of focus. They regard fragments as reals, rather than as symbolic devices to be directed toward the solution of a problem.

However, vocabulary among both the normal and the mildly abnormal tends to remain intact or even to increase with advancing years. The old person has a great fund of symbols and memories, a coral reef of knowledge to which he can add new layers with relative ease. The child, on the other hand, has the painful necessity of starting from scratch; every new concept of the tens of thousands that he normally acquires is a minor intellectual victory.

New laboratory procedures, Lewinian in type, are available for measuring that creeping intellective paralysis of old age—rigidity. Rigidity is the opposite of plasticity. It is compulsive in character. Having learned a certain method of approach, the rigid person is unable to relinquish it for another presumably better method. Objects, places, persons, concepts, conclusions and interpretations take on a special positive valence in relation to a time continuum. Rigidity is related to the degree of psychological differentiation. Few choices and patterns of experience characterize the young, the immature or the intellectually impoverished. Things are black or white, right or wrong, yes or no. The nuances, classifications and logical networks of the adult mind are taken on gradually. In the adult it is a form of deterioration to revert to dichotomous simplicities. Its indulgence calls for a substitution of loyalties and emotional responses for logical precision.

With respect to creative work in science, art, music, medicine and philosophy (as shown in the work of H. C. Lehman), the curves chronologically are long-drawn out. His major conclusion is that distinguished achievement will appear, for the most part, in the third decade. But a secondary finding, less often referred to, is the possibility of high achievement in all these areas up through the 50's and 60's. In one notable Lehman curve, depicting the average number of advances in medicine and public hygiene which were made during each five-year interval of the contributive line (based on 537 individuals and 801 contributions), there were entries for all the age intervals up to 90 years!

In curves of adult achievement there is found despair or hope, depending less on the demands of the objective data than upon the temperament of the reader. For some it is encouraging to note the existence of high scientific and artistic attainment in the sixth and seventh decades of life. What men have done, they may do again in intellectual as in other spheres.

Now in the 1940's, in an era that has stretched the period of infancy, lengthened man's labors while adding to his strength, and allowed its population curve to bulge in the direction of old age, we may expect the science of pediatrics to make room for the twin science of geriatrics.

Up through adulthood, we need studies of organic changes, particularly in the nervous sytem, that may affect or be affected by cultural experiences. Every word learned and every word lost is not only a mental and social phenomenon but an organic change, although no one-to-one relationship is implied.

If as full-grown and aging adults, we can through science maintain a firmer hold upon physical vigor while actively participating in affairs of the intellect, we shall be giving the organism its best chance. While a man cannot know from extrapolations of genetics or childhood development just what his limits of mental ability may be, he can learn to fight off the temptations to enfeeblement. For adults, as for youth, these debilitating forces can be recapitulated as follows:

1. Bad health conditions (e.g., nutritional, endocrinal or infectious) which may retard children and bring adults to a full stop.
2. The mechanisms of escape, retrospection and rigidity which result in partial or complete regression to more primitive intellectual patterns.
3. A lack of mental exercise—a failure to undertake new abstract learning as appropriate to adults as school and college are to the young.

The practical hope is that intellectual peaks may be reached and maintained on a less opportunistic basis by turning from a welter of fragments and postulates toward a systematic program of research in the biological and social sciences. Only this will discover the growth line of man as intellect, together with the factors and stimulations that tend to restore his vigor.

INTERSEXES IN DROSOPHILA PSEUDOÖBSCURA

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Diploid intersexes in Drosophila have been described in *D. simulans*[1] and *D. virilis*.[2, 3, 4] The purpose of the present note is to record the occurrence of a similar phenomenon in *D. pseudoöbscura* ("race *A*") and to evaluate its bearing on theories of sex determination.

Origin of the Intersexes.—In February, 1941, more than one hundred cultures were raised in which several males carrying the "sex-ratio" condition were crossed to unrelated normal females. The progeny of a male carrying the "sex-ratio" condition consists of daughters and few or no sons, regardless of the genetic constitution of his mate. This peculiar sex distribution arises because most of the spermatozoa of "sex-ratio" males contain an *X*- and no *Y*-chromosome. Some spermatozoa contain neither *X* nor *Y*; most of the rare sons of "sex-ratio" fathers are *XO* and are, therefore, sterile.[5] In the particular experiment under consideration several "sex-ratio" males and several normal females were placed in each culture and transferred from time to time in fresh culture bottles. In the series of cultures which developed in a cold room at 16°C. the total sex ratio was 98.8 per cent females and 1.2 per cent males. Two cultures coming from the same group of parents gave, however, abnormal results. One of them produced 115 females, 5 males and 122 intersexes; the other gave 119 females, 2 males and 144 intersexes.

All the males, though both externally and anatomically normal, proved to be sterile, presumably because they lacked *Y*-chromosomes. The intersexes were sterile because of the gross abnormalities in their reproductive organs. Some two dozen of the normal female sibs were outcrossed to unrelated males, partly in individual and partly in small mass cultures. Their offspring consisted of normal females and males; no intersexes appeared in F_2 and F_3 generations. The genetic condition responsible for the production of intersexes was, therefore, lost. Nevertheless, it is possible to infer with a very high degree of probability that the intersexuality was produced in this case by a dominant mutant gene present in one or more of the "sex-ratio" male parents; this gene transformed the females which inherited it from their father into intersexes. That the intersexes were transformed females and not transformed males was ascertained by cytological examination of three intersexual individuals (two having ovaries and one having rudimentary testes). They possessed normal diploid chromosome complements with two *X*-chromosomes. It is uncertain whether anything more than a coincidence was involved in the origin of

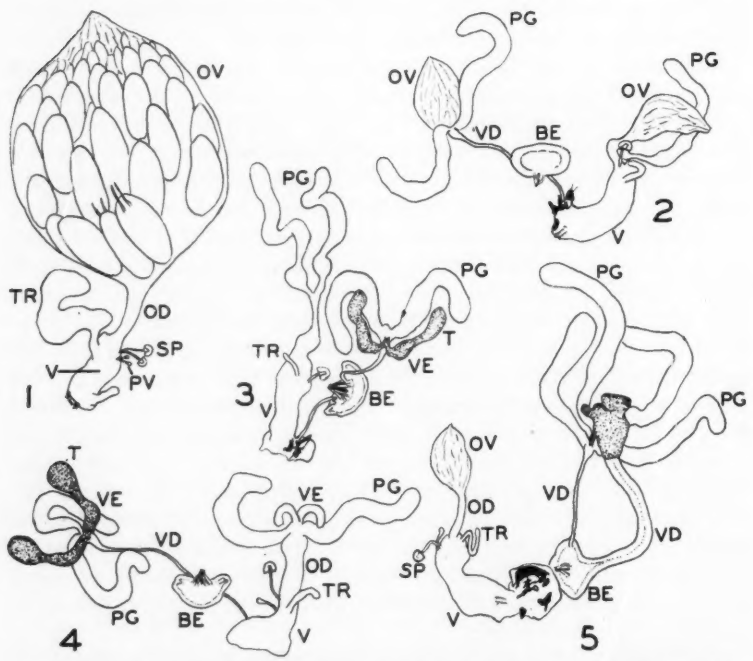
the intersex producing mutation in a male, or males, which carried also the "sex-ratio" condition. A causal relation is here very doubtful, since, except in the two cultures recorded above, no intersexes were found in the numerous "sex-ratio" cultures examined. This coincidence has, however, prevented the establishment of an intersex-producing strain. The fact that the intersexuality in *D. pseudoobscura* was almost certainly due to a dominant mutant gene is of some interest, since similar sex intergrades in *D. simulans*[1] and *D. virilis*[4] were caused by recessives.

Morphology of the Intersexes.—The external as well as the internal morphology of the intersexes is variable, although not to the same extent as in the *D. virilis* intersexes.[4] This lesser variability is not surprising since only two intersex-producing cultures were observed in *D. pseudoobscura*, while intersexuality in *D. virilis* was studied in strains with an assortment of genetic modifiers. Externally, the most female-like intersexes in *D. pseudoobscura* resemble normal females, except that their vaginal plates are smaller and somewhat displaced with respect to the plane of body symmetry (five such individuals were observed). A majority of the intersexes are definitely intermediate between males and females. The number of teeth in the distal sex comb varies from two to four, three being the mode; the proximal sex comb contains from four to six teeth, four and five being the most frequent numbers. In normal males of race *A* four to seven in the distal and six to nine teeth in the proximal sex comb are found.

The abdomen of Drosophila females has two more visible tergites than the male abdomen; in males, the morphological sixth and seventh tergites are fused, and the eighth tergite is either missing or included in the genital arch.[6] In the intersexes the sixth tergite is well developed and entire; the seventh is small and broken into two plates which do not reach the mid-dorsal line. Weakly chitinized traces of the eighth tergite can be identified in some intersexes.

The anatomy of about fifty intersexes was examined by dissection. Their reproductive organs are characterized by the presence of the normal number, i.e., two, of gonads, but of two, or even of three, sets of the genital ducts. The gonads may be ovaries containing apparently mature eggs (fig. 1; in this figure only one ovary attached to the oviduct is represented, while the other ovary, lying free in the body cavity, is not shown), or rudimentary ovaries with abortive egg strings (fig. 2), or ovotestes (the right gonad in fig. 5), or diminutive testes (figs. 3 and 4). As a rule, the two gonads of the same individual are similar: they are either both ovaries or both testes. However, in two individuals, one of which is shown in fig. 5, one gonad was clearly an ovary and the other an ovotestis. In contrast to the gonads, the two sets of genital ducts are invariably different in the same individual, one being more female-like and the other more male-like. In no case has a completely normal set of ducts of either sex been observed.

The most female-like intersex examined (Fig. 1) had two mature ovaries, one well-developed set of female ducts with two spermathecae and two parovaria, and a greatly broadened sac-like tubular receptacle. Its other set of ducts was reduced to a minute vagina-like pouch. In most intersexes the female set of ducts differs from the norm in having only a single



Figures 1–5, internal reproductive organs of diploid intersexes in *Drosophila pseudoobscura*. *BE*, sperm pump; *OD*, oviduct; *OV*, ovary; *PG*, paragonia; *PV*, parovaria; *SP*, spermathecae; *T*, testis; *TR*, tubular (ventral) seminal receptacle; *V*, vagina; *VD*, vas deferens; *VE*, vas efferens. Testes, vasa efferentia, seminal vesicles and ovo-testis (in Fig. 5) which are red in color in living specimens are shown stippled; note that the vasa efferentia in Fig. 4 to which no testes are attached are devoid of color, while the second pair of the vasa efferentia are colored.

spermatheca, a single parovarium and a short tubular receptacle. The presence of only a single spermatheca and parovarium instead of the normal two is of interest, since Lebedeff's photographs of the reproductive organs in the *D. virilis* intersexes show two spermathecae.[4] Another difference between the intersexes in *D. virilis* and *D. pseudoöbscura* is that in the latter, but apparently not in the former, the anterior portions of the female ducts

may display grotesque modifications in the male direction. Thus, the intersex shown in figure 3 has the upper portion of the vagina (above the tubular receptacle) broadened and somewhat resembling the sperm pump of the male, the oviduct modified in the direction of the vas deferens and ending in what are unquestionably male paragonia. The transformation is even more pronounced in the specimen shown in figure 4. Here the oviduct carries at its inner end not only a pair of apparently normal paragonia but also fairly normal vasa efferentia.

In some of the intersexes the male ducts differ from normal only by their smaller size (Figs. 3, 4). Among the male organs, the sperm pump appears to be most sensitive to the feminizing influences of the intersexual constitution. Next, the vas deferens becomes broader than normal, and comes to resemble an oviduct, retaining, nevertheless, its paragonia. In the intersex shown in figure 5 one may see a set of female and a set of male ducts, and also a third set which can be described only as intermediate between female and male. This intersex has four enlarged paragonia. If an intersex has ovaries attached to the vasa efferentia, the latter assume the red coloration characteristic of the vasa efferentia in normal males. This fact is of interest in connection with the problem of the origin of this coloration. Dobzhansky[7] found colored vasa efferentia in gynandromorphs of *D. simulans* which possess ovaries but no testes, while Stern and Hadorn[8] proved that the colored portion of the vas efferens normally arises from the testicular sheath. A possible solution of this apparent contradiction is that the ovary possesses a sheath similar to that of the testis, but which develops no pigment unless it comes in contact with a vas efferens. The observed structures of the genital ducts in the intersexes of *D. pseudoobscura* may throw some light also on a purely morphological problem, namely that of the homologies of the parts of the female and male reproductive systems in Drosophila. From our observations it would appear that the lower portion of the vagina in the female corresponds to the ejaculatory duct in the male, the upper portion of the vagina to the sperm pump, and the oviduct to the vas deferens. Females have no homologue of the paragonia, and males no homologues of the spermathecae, parovaria or the ventral tubular receptacle.

The presence in the intersexes of two sets of genital ducts and only one pair of gonads indicates that in the larvae from which these intersexes develop there must be either two imaginal discs from which the genital ducts and the external genitalia normally develop[6], or else that a single disc becomes eventually split into two which subsequently give rise each to a separate system of ducts. The external genitalia of the intersexes are what one could expect them to be on the basis of the above views. Except in the extreme female type intersexes, each individual has two sets of genitalia, one of them distinctly more female-like and the other male-like, but neither

of them complete. Most intersexes have an asymmetrical genital arch which is more or less normal on one side but rudimentary on the other; a misshapen penis; a more or less well-developed or rudimentary vaginal plate or two plates; and a single anal tubercle of the male type. The position of these organs with respect to each other is highly variable, so that no two individuals have similarly built genitalia. In some intersexes the whole system of the genitalia fails to come out to the body surface, evidently because of non-eversion of the imaginal disc.

Discussion.—The diploid intersexes known in *Drosophila simulans*, *D. virilis* and *D. pseudoöbscura* differ from the triploid ones in *D. melanogaster*. The diploids have characteristically two systems of genital ducts and external genitalia, the developmental basis being here a reduplication or a splitting of the genitalic imaginal disc; the triploids, with rare exceptions,[6] have a single set of ducts and of genitalia intermediate in structure between female and male. This profound structural difference cannot be accounted for by the occurrence of triploid intersexes in *D. melanogaster* and of the diploid ones in other species. One of us has observed a spontaneously arisen triploid intersex in *D. pseudoöbscura* (the chromosome-complement checked cytologically) and three such intersexes in hybrids between *D. pseudoöbscura* and *D. miranda* (cytologically not examined). Their morphology resembled that of the triploid intersexes in *D. melanogaster* (types II and III[6]).

Goldschmidt's conception of a sexual turning point (the "time law") fits reasonably well the facts known about the triploid intersexes,[6] but to account on the same basis for the structures of intersexes that are diploid one must make the assumption that in the latter the two sets of genital ducts always develop at rates so different that the turning point finds one of them physiologically much younger than the other. Since the two systems of ducts are frequently equally well developed, the morphology of the adult diploid intersexes gives little basis for such an assumption. Owing to the presence of two sets of reproductive organs, one approaching the female and the other the male type, the diploid intersexes could be termed also hermaphrodites. We prefer the former term, because the duplication, or even the triplication, involves only the derivatives of the genitalic imaginal disc, i.e., the genital ducts and the external genitalia, but does not involve the gonads. Nevertheless, it is possible to conceive that a mutant producing a condition of this sort, if it were to arise in a strain possessing genetic modifiers making the two sets of genital ducts functional, could become the nucleus of a genotype transforming a bisexual species into a hermaphroditic one. The type of intersexuality found in triploid Drosophila and in diploid Lymantria has, on the other hand, nothing to do with hermaphroditism.

Diploid intersexuality in *D. simulans* and *D. virilis* is known to be caused by mutation of apparently a single gene, and the same is virtually certain for *D. pseudoöbscura*. The rôle of the normal allele of this gene in sex determination is, however, by no means established. According to the interpretation advanced by Lebedeff,[3,4] the locus at which the intersex-producing mutation arose in *D. virilis* is that of "the gene for maleness," the mutant allele being more efficacious than the normal one, and thus transforming genetic females (i.e., individuals possessing two *X*-chromosomes with two normal "genes for femaleness") into intersexes. This interpretation is not the only possible one. In the first place, the fact that a mutant allele of a gene causes a modification of the development in the direction of maleness does not prove that the normal allele of the same gene is also a gene for maleness, or in fact that it has anything to do with sex determination. Furthermore, the locus at which the mutant genes producing diploid intersexuality arise need not be the main or the only gene for maleness (the "male sex differentiator"). Dobzhansky and Schultz[9] have shown that the female determining effect of the *X*-chromosome in *D. melanogaster* is a result of coöperation of several, presumably numerous, genes rather than that of a single female sex differentiator. Their results were questioned by Goldschmidt.[10] Bedichek Pipkin[11] has recently obtained an unimpeachable confirmation of the multiplicity of sex-determining genes in the *X*-chromosome of *D. melanogaster*, and Goldschmidt[12] has taken the position that since, in his opinion, discrete genes do not exist the alternative of a single versus multiple sex genes is meaningless. There is no evidence of singleness or multiplicity of the male determiners in the autosomes of any species of Drosophila, and the available data on diploid intersexuality do not come anywhere near to furnishing such evidence. On theoretical grounds, it is perhaps easier to visualize the phylogenetic transition from hermaphroditism to bisexuality as being caused initially by only a single or few genes. The genetic mechanism underlying a given organ or function may, however, undergo changes in evolution; a function originally determined by a single gene may eventually become served by many cooperating genes. Hermaphroditism is extremely rare in the class Insecta; if the living representatives of this class had hermaphroditic ancestors, this ancestry is very remote. The multiple causation of the sex-determining mechanism in Drosophila is, thus, in no way unexpected.

Summary.—Diploid intersexes in *Drosphila pseudoöbscura* are described. Most of them have two sets of genital ducts and external genitalia but only one pair of gonads. One of the sets of the ducts and the genitalia is almost always more female-like and the other more male-like. The genetic causation of the intersexuality in this case is most probably a single dominant gene transforming diploid females into intersexes. It is argued that the normal allele of this gene need not be regarded as the single gene for male-

ness nor even as being involved in any way in the mechanism of sex determination.

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THE ORIGIN OF JERKER, A NEW GENE MUTATION OF THE HOUSE MOUSE, AND LINKAGE STUDIES MADE WITH IT

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In June, 1938, a woman who raises mice for her own amusement brought to one of us (Grüneberg) a dancing adult female mouse which had been given to her by a schoolboy. The mouse was of the *Mus musculus* type and not appropriate to keep with her waltzers which were *Mus bactrianus*. It was, however, pregnant, she claimed, by one of her genuine Japanese waltzers, yet the litter consisted of three perfectly normal animals, thereby indicating that the mutation was distinct from waltzing.

Such a genetic test was apparently the only way to distinguish waltzers and jerkers, as the new mutation was named. The age of onset of the jerker characteristics is about 11 or 12 days. At this age signs of poor balance, shaking the head and traveling in a circle become visible, but not until the animal's eyes are open and they become more active at 14 days can the jerker animals be distinguished from the normals with certainty. One good way to tell is to hold the animal by the tail just off the table. The jerkers twist and turn their whole bodies while normals stretch out and try to reach the surface beneath. So far as we could tell, jerkers also are stone-deaf as they show no reaction to a sharp metallic click as do normals—a fact which suggests that the inner ear is abnormal in some way. The jerkers whirl in both directions, shake their heads and back up instead of running ahead. Often the adults when aroused leap and twist about in

somersaults much as waltzers do. The animals breed poorly chiefly because the mothers do not nurse well. In all these respects the new mutation resembles waltzing and the shaker mutations. Accordingly crosses were carried out to test the individuality of the mutation and also its linkage relations. These crosses are described below and the actual data are given in table 1.

In the first place, in order to distinguish the new mutation from other similar ones, a homozygous jerker animal was crossed with waltzers again and with shaker-2 animals. No offspring exhibiting any kind of dancing abnormalities resulted from these crosses. Three different waltzing (*vv*)

TABLE 1

TABLE OF LINKAGE DATA AND CROSSOVER PERCENTAGES OF JERKER GENE

GENE	MATING	*Xje*	*xJe*	*Xje*	*xje*	NO. MICE	CROSSOVER PERCENTAGE
a	F_2 repulsion	37	21	16	6	80	44.2 ± 8.8
	MC repulsion	58	60	17	16	151	48.5 ± 8.7
b	F_2 repulsion	55	17	15	2	89	38.3 ± 7.8
	F_2 coupling	29	12	10	5	56	47.3 ± 9.6
c	F_2 coupling	12	9	5	3	29	24.4 ± 9.4
Ca	*BC* to *jejecaca* coupling	31	33	36	21	121	57.0 ± 4.6
d se	F_2 repulsion	146	46	45	9	246	43.6 ± 5.1
f	*BC* to *JeJeff* repulsion	17	4	14	5	40	55.0 ± 7.9
ln	*BC* to *JeJelnln* repulsion	9	9	17	10	45	42.2 ± 7.9
p	F_2 repulsion	149	42	39	12	242	51.2 ± 4.8
Re	*BC* coupling	18	20	15	15	68	51.5 ± 6.1
s	*BC* to *JeJess* repulsion	9	9	21	6	45	33.3 ± 7.5
	F_2 coupling	132	40	43	14	229	49.0 ± 4.9
sh-2	*BC* to *JeJesh-2sh-2*	15	6	13	6	40	47.5 ± 7.9
T^1	*BC* to *jejett* coupling	2	47	2	51	102	
v	*BC* to *JeJevv* repulsion	12	6	18	9	45	46.7 ± 7.5
W	*BC* to *jejewv* coupling	20	41	26	34	121	55.4 ± 7.5
wa-1	*BC* to *JeJewa-1wa-1* repulsion	7	11	14	13	45	44.4 ± 7.5
wa-2	*BC* to *JeJewa-2wa-2* repulsion	13	8	11	8	40	52.5 ± 7.9

mothers produced 12 normal young; 4 different shaker-2 mothers (*sh-2 sh-2*) produced 18 normal young, thus definitely establishing the jerker mutation as distinct from *v* and *sh-2*. In a cross with pink-eye (*p*) and albinism (*c*) in later tests, the jerker gene showed no linkage with these two characters, and hence cannot be identical with shaker-1 which is linked with both of these.

When the mutation was thus definitely known to be at a new locus, linkage tests were carried out against as many of the known chromosome markers as were available at the Jackson Laboratory. These markers included all the known linkage groups except *r si* and all the known single genes except *dw* and *hy-1*. This meant that out of a possible sixteen markers, thirteen were tested.

The genes used in these crosses are carried at the Jackson Laboratory in four stocks of mice. In the first of these, the *P* stock, inbred for twenty generations, occur five recessive genes *a*, *b*, *p*, *d*, *se*, the last two being very closely linked. The straight F_2 ratio had to be used in this case since the recessive necessary for a backcross of all the genes would be very hard to obtain, and using one gene at a time to backcross would nullify the value of the stock. The plan was simply to cross the *XXjeje* male with the *xxJeJe* females giving the double heterozygote *XxJeje*. This F_1 when interbred would give the normal 9:3:3:1 phenotypic ratio in the F_2 population if no linkage existed. The jerker males used in this cross happened to be heterozygous for *a* and the data had to be separated into two classes, according to the F_1 animals. Some of these would be the double heterozygotes; others would be homozygous for non-agouti. In the latter case the F_2 generation forms the same phenotypes as the straight F_2 but in the ratio of 3:3:1:1 and only the 1:1 classes can be used in determining the crossover genotypes. We have called this a "mixed backcross," abbreviated *MC*. As can be seen from the data in the table, *je* is not linked with any of these genes.

In another stock of mice, three dominant mutations are carried: caracul coat (*Ca*), dominant spotting (*W*) and fused (T^f). To test for these the straight backcross of the multiple heterozygote to the multiple recessive was used, giving a 1:1:1:1 ratio. Unfortunately the fused-tail character showed up in only four animals because of overlapping in this particular stock. This cross should be repeated.

The remainder of the genes *wa-1*, *wa-2*, *s*, *ln*, *f*, *v*, *sh-2* and *w*, all recessives, are carried in two stocks of mice. The same plan was used in each case. It is difficult or impossible to distinguish *v* and *sh-2* phenotypically from jerker. Hence the back-cross animals had to be tested genetically. The plan of the cross:

		JERKER	×	STOCK MICE	
		jejeXX		*JeJexx*	
F_1		*JejeXx*	×	*JeJexx*	
BC	*JeJeXx*	*JeJexx*		*JejeXx*	*Jejexx*

This is essentially the cross described by Castle[1] for testing the linkage between lethal genes.

About 50 back-cross females were outcrossed with jerker animals to determine whether they were homozygous *JeJe* or heterozygous *Jeje*. About one-fifth of these animals failed to nurse their litters due to an overdose of detrimental mutations. In the case of homozygous animals, 7 normal offspring were considered proof of the *JeJe* formula. Here as before no linkage was apparent.

One more character, rex (*Re*), was tested with negative results for linkage with Jerker. The straight backcross of the double heterozygote to the double recessive was used.

From these data we may conclude that no linkage exists with any of the characters tested, except that the data with respect to the *T* locus are inconclusive. Very likely, then, the jerker mutation can be used to mark a different chromosome. *Dw*, *hy-1* and the linkage group *r si* are the only markers as yet untested. Unless one of these should show linkage with *je*, a new chromosome marker will be established.

The authors would like to express their appreciation to Dr. Dunn for his assistance in bringing the jerker mice from England to the United States, and for maintaining them for a while in his laboratory. They wish also to thank Dr. Reed for providing space in his animal room at Harvard University where some of the crosses were carried out.

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*GENIC EFFECTS ON SERUM PROTEINS**

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A previous report[1] from this laboratory has described the segregation of one or more so-called *species-specific* components of the serum proteins of Pearlneck (*Streptopelia chinensis*), following backcrosses to Ring dove (*St. risoria*) of species hybrids and back-cross hybrids from the mating of Pearlneck and Ring dove. Further, two back-cross individuals, obtained by mating to Ring dove hybrids of pigeon and Ring dove, have been shown to possess in their respective sera at least one antigen specific for pigeon, qualitatively different from that in the serum of the other.[2] Complete references to related investigations may be found in the bibliographies of the earlier reports.[1, 2, 6]

These findings are in accordance with the results of investigations of the segregation of cellular antigens in the erythrocytes of several dove and pigeon species and their hybrids and back-cross hybrids, which gave evidence of genic influence on the antigens of the red blood cells.[3–5] However, the genes, affecting the species-specific cellular antigens in the Pearlneck and pigeon, respectively, appear to be independent in action from those affecting the species-specific antigens of the serum.[1, 2]

The present paper submits corroborative evidence of the earlier findings. In this series of tests, the species involved were the Pearlneck and the Sene-

gal (*St. senegalensis*) as well as offspring of backcrosses of species hybrids to Senegal. The sera of the various back-cross birds were tested to determine the segregation of antigens, specific for Pearlneck, as contrasted with Senegal.

Materials and Methods.—The immunological techniques employed herein were virtually the same as those described in detail in previous reports.[1, 2, 6] In brief, rabbits were inoculated intravenously with the serum of Pearlneck. The anti-Pearlneck sera thereby produced were tested by the ring-precipitin test, using as antigen the sera of the two species and of

TABLE 1

PRECIPITIN REACTIONS WITH THREE ANTI-PEARLNECK SERA, PREVIOUSLY ABSORBED WITH SENEGAL SERUM

SERA	ANTI-PEARLNECK SERUM NUMBER 227S5	267S1	198S3	PRESENCE OR ABSENCE OF SPECIFIC PEARLNECK CHARACTERS IN RED BLOOD CELLS
Pearlneck	64[1]	32	16+	+
Senegal	0	0	0	0
(*a*) Reactions of Sera of First Back-cross Generation Hybrids				
D631E	16+	16	4+	0
D820L	16+	8	4+	+
D820V2	4	4	2	+
E11U	4	4	4+	+
E11V	16+	16+	4+	+
E11Z	4	4	4+	+
(*b*) Reactions of Sera of Second Back-cross Generation Hybrids				
D967Q	16+	8	4+	+
D967V	0	0	0	+
D967Y	8	16+	4+	+
D967L2	16+	16+	4+	0
D967N2	0	0	0	0
D967Y2	16+	16+	4+	0
D967J3	16+	16+	4+	+
E132J2	0	0	0	0

[1] The numbers represent the highest dilution of serum at which a definite precipitate was visible. A plus (+) sign following a number indicates a strong reaction at the final dilution; presumably, a reaction would have occurred at higher dilutions.

individuals of the back-cross progeny. In these tests, which were carried out in precipitin tubes of 2-mm. diameter, the antigen in its successive dilutions was carefully layered above the antiserum. A "positive" reaction between the antigen and antiserum was indicated by the appearance of a well-defined "ring" of precipitate at the antigen-antiserum interface. The absence of a ring indicated that no definite reaction had occurred. The absorption of antibodies was carried out as in the earlier experiments,[1, 2, 6] extreme care being taken to prevent overabsorption. In these investiga-

tions, the anti-Pearlneck sera from three different rabbits were used, and are designated in table 1 as antisera Nos. 198S3, 227S5 and 267S1.

The back-cross individuals were produced by mating two species—hybrid females, (D429H and D429U2), offspring of a Pearlneck male and Senegal female, to Senegal, producing the first back-cross generation, or $^1/_4$ Pearlneck, $^3/_4$ Senegal. D429H is the parent of D631E and of the two birds listed as of family D820; D429U2 is the parent of family E11, as listed in table 1. Two of the first back-cross birds (D820A and D820L) were mated to Senegal, giving rise to the second back-cross generation, or $^1/_8$ Pearlneck, $^7/_8$ Senegal. The tests herein described were made on the sera of six birds from the first, and of eight birds from the second back-cross generation. Unfortunately, no species hybrids ($^1/_2$ Pearlneck, $^1/_2$ Senegal) were available for testing as to the content in their sera of the antigens of Pearlneck and Senegal. However, since the backcrosses had been made only to Senegal, the segregation of antigens to be studied in the back-cross individuals would be of those particular to Pearlneck, and such antigens must then have been present in the sera of the species hybrids.

Results.—When various anti-Pearlneck sera were tested directly with the sera of Pearlneck and Senegal doves, the reactions of the sera of the two species were found to be essentially the same. The highest dilution of antigen at which reactions occurred was with some antisera as much as 1:25,600. Other antisera gave lower reactions. By virtue of these direct precipitation tests, it was impossible to differentiate the sera of the two species. However, differentiation of the serum of Pearlneck from that of Senegal was readily accomplished by absorbing certain anti-Pearlneck sera with serum of Senegal, and then testing the "reagent" with the serum of both Senegal and Pearlneck. When this test was made, the Senegal serum gave no reaction at dilutions of 1:2, 1:4, 1:8 and 1:16; whereas the Pearlneck serum reacted strongly at all these dilutions, and up to serum dilutions of 1:32 and 1:64. This reaction shows that the antiserum for Pearlneck contained two or more qualitatively distinct antibodies, of which at least one was capable of interacting with Pearlneck and not with Senegal serum. Whether the one or more antigens in the serum of Pearlneck which distinguish it from the serum of Senegal were due to determinant groups, as is usually assumed, or to similar but not identical structures of the protein molecules, cannot be definitely stated. Arguments on both sides of the question have been discussed by Landsteiner and van der Scheer.[8] Following the same terminology in this that has been used in former papers, the antigenic complex of Pearlneck which distinguishes it from Senegal will be termed "*species-specific*," and that which in the two species is similar if not identical will be called "common."

Anti-Pearlneck serum, therefore, following absorption with Senegal serum, is capable of detecting one or more antigenic structures in Pearlneck

serum which are specific for the Pearlneck species, as contrasted with Senegal. If, then, these antigens specific to Pearlneck are heritable, they may be expected to appear in the sera of birds resulting from backcrosses to Senegal. Therefore, the absorbed reagents were tested with the sera from fourteen back-cross individuals with results as given in table 1. The serum of each bird, usually at dilutions of 1:2, 1:4, 1:8 and 1:16, was tested against the three different reagents indicated in the table, with adequate controls as to the completeness of the absorption by Senegal serum. The three reagents gave virtually the same reactions with the sera of these 14 individuals.

It will be seen in the table that the serum of each of the six individuals of the first back-cross generation gave positive reactions with each of the three reagents. Since these tests show the presence of an antigenic complex particular to Pearlneck, and the species hybrids, although not tested, were from the mating of a Pearlneck male, the possibility of cytoplasmic transmission of these serum constituents at least to the species hybrid can presumably be disregarded. If one or more genes on a chromosome (originally derived from the Pearlneck parent) of the two species hybrid females together produced an effect upon the serum proteins, a 1:1 ratio of birds possessing and not possessing the particular antigenic complex would be expected in the progeny of the first backcross. Likewise if one or more genes on each of two such chromosomes produced different effects, four kinds of offspring would be expected in the first back-cross generation, as previously explained. The number of offspring (six) in the first back-cross generation is too few to state whether more than one antigenic constituent is involved. At present we have no evidence which would indicate whether the antigenic complex of D820L, for example, is the same as that found in the serum of D631E or E11V. Experiments are now in progress to determine to what extent these various serum antigens are the same or related. One of these back-cross birds (D820L) was the female parent of the D967 family. The serum of each of five of the seven offspring of this mating gave a positive reaction and that of two gave no observable precipitate with the three reagents for specific Pearlneck antigens. Thus within this family there was a definite segregation of the Pearlneck specific antigens which were contained in the back-cross parent (D820L), five of the offspring receiving part or all of this particular species-specific antigenic complex of the parent and two not receiving it as would be expected if one or more genes on a single chromosome produced such an effect. The other back-cross hybrid, E132J2, possessed in its serum no demonstrable antigens specific for Pearlneck. However, since the serum of its back-cross hybrid parent (D820A) was not available for testing, no information can be derived from this test.

This experiment corroborates the findings in the Pearlneck/Ring dove

hybrids and back-cross hybrids. And similarly, these results cannot be rationally explained without assuming that genes on one or more Pearlneck chromosomes have produced the specific Pearlneck antigens which segregated in the back-cross generations.

Correlation of Pearlneck-Specific Components of the Serum and Blood Cells.—Earlier studies have been made to determine the inheritance of the Pearlneck specific antigens in the blood cells of hybrids and back-cross hybrids of the Pearlneck/Senegal cross.[7] It is a matter of some interest, therefore, to determine whether the same genes produce antigens, particular to Pearlneck, in the red blood cells and in the serum as well. If the respective antigens are produced by different genes, the question arises as to whether the causative genes are linked or are borne on different chromosomes.

The fifth column of table 1 shows the presence or absence of Pearlneck specific characters in the blood cells of the various back-cross birds. By comparing the data in this column with those in columns 2–4, inclusive, certain points become evident.

The six individuals of the first back-cross generation all possessed Pearlneck specific antigens in their sera, and all except one (D631E) possessed characters specific to Pearlneck in their red blood cells. Therefore, we may reasonably conclude that the serum reactions are not due to substances produced in the serum by a breakdown or secretion of the corpuscles. Furthermore, the presence of an antigen specific to Pearlneck in the serum of a back-cross individual and the absence of a cellular antigen in the same bird show that different genes are involved in the production of the species-specific antigens in the serum and blood cells, respectively. Both of these conclusions are substantiated by the data concerning the second back-cross hybrids.

As given above, D820L was the hybrid parent of the D967 family and within this family there was a definite segregation of the corpuscular characters, as well as of antigens of the serum. Thus, three birds (Q, Y, J3) possessed both specific corpuscular characters and specific Pearlneck serum antigens; two birds (L2, Y2) did not have a specific cellular substance, but did have specific serum antigens; one bird (N2) possessed neither Pearlneck specific cellular nor serum antigens; and one bird (V) possessed specific cellular characters but not specific serum antigens. The other member of the second back-cross progeny (E132J2) had no demonstrable antigens specific to Pearlneck in either cells or serum. It appears from the evidence that the antigens specific to Pearlneck in the cells and in the serum, respectively, are determined by different genes, either on separate chromosomes or loosely linked. These results parallel those obtained in previous studies.[1, 2]

Summary and Conclusions.—The antigens in the serum of Pearlneck, specific for that species as contrasted with Senegal, have been found to

segregate in back-cross individuals in accordance with genetic expectation. The results of this and previous investigations show beyond reasonable doubt that the species-specific qualities of the serum proteins are determined by gene action and suggest that the total protein complex of the serum is likewise determined by genes.

The genes that in Pearlneck produce the serum antigens are not the same as those that produce the cellular antigens, and possibly are not on the same chromosomes. These findings corroborate the results of parallel investigations of the sera and cells of back-cross hybrids of other combinations of species of doves and pigeons.

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† Assistance in the production of the hybrids was given by Dr. Geo. W. Woolley.

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ON THE MOTION OF VORTICES IN TWO DIMENSIONS—I. EXISTENCE OF THE KIRCHHOFF-ROUTH FUNCTION

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1. *Introduction.*—Kirchhoff[1] was the first to establish the existence of "a stream function giving the motion of vortices" in an *unbounded* region. Later, in 1881, Routh[2] enunciated a theorem regarding the transformation of a function of that nature for the case of a *single* vortex moving in a *bounded* region. No proof was given and the existence of such a stream function was not established.[3] In 1921, Lagally[4] established the existence of this "*Routh's stream function*" and the more general "*Kirchhoff's path function*" for a *simply connected bounded* region. An independent proof for the case of a single vortex in such a region was also given by Masotti[5] in 1931, by using the Green function of the first kind. However, the most general case of the motion of a number of vortices in a *multiply connected*

region is not covered by their work. The present article establishes the existence of the "*Kirchhoff-Routh function*"[6] for the general case. The proof makes use of a generalized Green function and may therefore be regarded as a generalization of Masotti's work. Explicit formula of this function is also given. A more detailed treatment of this work will appear elsewhere.

2. *Statement of the Problem.*—Consider a number of isolated free vortices of strengths κ_i $(i = 1, 2, ..., n)$ at the points $P_i(x_i, y_i)$ $(i = 1, 2, ..., n)$ in an incompressible fluid moving irrotationally in a region R. This region has a number of internal boundaries C_k $(k = 1, 2, ..., m)$ and it is (a) bounded externally by a closed curve C_0, or (b) unbounded from the outside, or (c) limited by curves C_0 extending to infinity.

If the ordinary stream function of fluid motion

$$\psi = \psi(x, y; x_1, y_1; \ldots; x_n, y_n) \tag{2.1}$$

is known (which is obviously independent of the time t explicitly), the components of velocity of the ith vortex $(i = 1, 2, ..., n)$ are given by

$$\frac{dx_i}{dt} = u_i = -\left(\frac{\partial \psi_{(i)}}{\partial y}\right)_{P_i}, \quad \frac{dy_i}{dt} = v_i = \left(\frac{\partial \psi_{(i)}}{\partial x}\right)_{P_i} \tag{2.2}$$

where

$$\psi_{(i)} = \psi - \frac{\kappa_i}{2\pi} \log r_i, \quad r_i = \sqrt{(x - x_i)^2 + (y - y_i)^2}, \tag{2.3}$$

and the suffixes P_i denote that the results of differentiation are to be evaluated at the point P_i. For the case where the region R has no solid boundaries and where steady streaming is absent, Kirchhoff[1] has shown that there exists a function

$$W = W(x_1, y_1; x_2, y_2; \ldots; x_n, y_n), \tag{2.4}$$

such that the motion of the ith vortex is given by

$$\kappa_i \frac{dx_i}{dt} = \kappa_i u_i = -\frac{\partial W}{\partial y_i}, \quad \kappa_i \frac{dy_i}{dt} = \kappa_i v_i = \frac{\partial W}{\partial x_i}. \tag{2.5}$$

The object of this article is to show that this result of Kirchhoff can be generalized to the motion of vortices in a region R of the general type described above. In another article, we shall derive the law of transformation of the *Kirchhoff-Routh function* W under a conformal transformation.

We shall first define a generalized Green function particularly suited to the study of vortex motion. The essence of this paper, like Masotti's work, lies in the application of the reciprocity property of a properly defined Green function. (Cf. equations (3.5) and (3.6)).

3. *The Green Function.*—Let us define a function $G(x, y; x_0, y_0)$ with respect to two points $P(x, y)$ and $P_0(x_0, y_0)$ in the region R by the following three conditions.

(i) The function

$$g(x, y; x_0, y_0) = G(x, y; x_0, y_0) - \frac{1}{2\pi}\log r_0 \qquad \left(r_0 = \sqrt{(x - x_0)^2 + (y - y_0)^2}\right) \quad (3.1)$$

is harmonic with respect to (x, y) throughout the region R including the point P_0; thus,

$$\frac{\partial^2 g}{\partial x^2} + \frac{\partial^2 g}{\partial y^2} = 0. \quad (3.2)$$

(ii) If $\partial G/\partial n$ is the normal derivative of the function G on a curve (with x, y as variables), then

$$G = A_k \text{ on } C_k, \quad \int_{C_k'} \frac{\partial G}{\partial n}\, ds = 0 \quad (k = 1, 2, \ldots, m) \quad (3.3)$$

for each of the inner boundaries C_k; where ds is an element of arc of the closed analytical curve C_k', which encloses C_k but neither the other boundary curves nor the point P_0. The positive normal to C_k' is drawn toward C_k and the positive direction of C_k' is taken so that the main part of R (including P_0) lies to its left. Similar positive directions are used for any other curve.

(iii*a*) If the region R has a closed outer boundary C_0, then

$$G(x, y; x_0, y_0) = 0 \quad \text{over } C_0. \quad (3.4a)$$

(iii*b*) If the region R extends to infinity in all directions, the function $G(x, y; x_0, y_0)$ behaves as follows:[7]

$$\left.\begin{aligned} G(x, y; x_0, y_0) &= \frac{1}{2\pi}\log r_0 + O\left(\frac{1}{r_0}\right), \\ \frac{\partial G}{\partial s} &= O\left(\frac{1}{r_0^2}\right), \frac{\partial G}{\partial n} = \frac{1}{2\pi r_0} + O\left(\frac{1}{r_0^2}\right), \end{aligned}\right\} \text{ over a very large circle of radius } r_0. \quad (3.4b)$$

where $\partial G/\partial s$ is the tangential derivative along the circle.

(iii*c*) If the region R has boundaries C_0 extending to infinity, the function $G(x, y; x_0, y_0)$ behaves as follows:[7]

$$\left.\begin{aligned} G(x, y; x_0, y_0) &= O \quad \text{over } C_0, \\ G(x, y; x_0, y_0) &= o(1) \quad \text{over a very large circle of radius } r_0. \end{aligned}\right\} \quad (3.4c)$$

Koebe[8] established the existence and uniqueness of this Green function G by resolving it into a linear combination of two sets of basic functions: (*a*) the Green function of the first kind and (*b*) the set of harmonic functions each of which takes the value unity on a particular one of the boundary

curves and the value zero on all the others. With the help of this resolution, the present writer finds it possible to prove the symmetry property of this Green function by using standard methods.[9]

We summarize the results in the following lemma.

LEMMA I. *The function* $G(x, y; x_0, y_0)$ *defined by the conditions* (3.2)–(3.4) *exists uniquely, and is a generalized Green function satisfying the reciprocity property*

$$G(x, y; x_0, y_0) = G(x_0, y_0; x, y). \tag{3.5}$$

The reciprocity property immediately leads to the following important result (cf. (3.1)):

$$\left.\begin{aligned} \frac{\partial}{\partial x_0} g(x_0, y_0; x_0, y_0) &= 2 \lim_{P \to P_0} \frac{\partial}{\partial x} g(x, y; x_0, y_0), \\ \frac{\partial}{\partial y_0} g(x_0, y_0; x_0, y_0) &= 2 \lim_{P \to P_0} \frac{\partial}{\partial y} g(x, y; x_0, y_0). \end{aligned}\right\} \tag{3.6}$$

4. *Kirchhoff's Equations.*—Let us now apply our function G to the hydrodynamical problem of vortex motion with the stream function (2.1).

The motion given by the stream function

$$\Psi = \kappa_0 G(x, y; x_0, y_0) \tag{4.1}$$

may be called the motion *due* to a vortex κ_0 at the point $P_0(x_0, y_0)$. It is a possible potential motion in the region R with the required singularity, and has no circulation around any one of the inner boundaries. Furthermore, if the region R extends to infinity, the flow *across* an arc of the circle $r_0 =$ constant (contributing to outward flux) approaches zero and the flow *along* it (contributing to circulation) is finite (or approaches zero), as r_0 becomes infinite.

If we subtract the stream functions *due* to all the vortices from the complete stream function (2.1), the remainder is a stream function giving a possible potential motion in the region R. Now, this motion is uniquely defined when the circulation around each of the curves C_k and the fluid velocity at infinity are given. Since these conditions are the same for the complete stream function as for this part, this motion is actually independent of the (variable) positional coordinates (x_i, y_i) of the vortices. It depends on the (constant) strengths κ_i, only if the conditions defining it happen to be so. We may therefore call it the motion "*due* to outside agencies."

We summarize our results in the following basic lemma.

LEMMA II. *If* n *vortices of strengths* κ_i $(i = 1, 2, \ldots, n)$ *are present in an*

incompressible fluid at the points $P_i(x_i, y_i)$ $(i = 1, 2, ..., n)$ *in a general region bounded by fixed boundaries, the stream function of fluid motion is given by*

$$\psi(x, y;\ x_1, y_1,\ ...;\ x_n, y_n) = \psi_0(x, y) + \sum_{i=1}^{n} \kappa_i G(x, y;\ x_i, y_i), \quad (4.2)$$

where the properties of $G(x, y;\ x_i, y_i)$ *are given in Lemma I, and* $\psi_0(x, y)$ *is the stream function of the motion due to outside agencies, independent of* $P_i(x_i, y_i)$ *(and of* κ_i*).*

With this result at hand, we can at once establish the existence of the Kirchhoff-Routh function.

THEOREM I. *For the motion of vortices of strengths* $\kappa_i (i = 1, 2, ..., n)$ *in a general region R bounded by fixed boundaries, there exists a Kirchhoff-Routh function* $W(x_1, y_1;\ x_2, y_2;\ ...;\ x_n, y_n)$ *such that*

$$\left.\begin{aligned} \kappa_i \frac{dx_i}{dt} &= \kappa_i u_i = -\frac{\partial W}{\partial y_i}, \\ \kappa_i \frac{dy_i}{dt} &= \kappa_i v_i = \frac{\partial W}{\partial x_i}, \end{aligned}\right\} \quad (4.3)$$

where $P_i(x_i, y_i)$ $(i = 1, 2, ..., n)$ *are the instantaneous positions of the vortices. The function W is given by*

$$W = \sum_{i=1}^{n} \kappa_i \psi_0(x_i, y_i) + \sum_{\substack{i,j=1 \\ (i>j)}}^{n} \kappa_i \kappa_j\, G(x_i, y_i;\ x_j, y_j) + \frac{1}{2} \sum_{i=1}^{n} \kappa_i^2 g(x_i, y;\ x_i, y_i). \quad (4.4)$$

This can be at once verified by comparing the results for u_i and v_i obtained from (4.3), (4.4) and (3.6) with those obtained from (2.2), (2.3) and (4.2). We note that the system of *Kirchhoff's equations* (4.3) is a Hamiltonian system of differential equations in the set of variables $\sqrt{\kappa_i}x_i$ and $\sqrt{\kappa_i}y_i$, $(i = 1, 2, ..., n)$.

It is not difficult to show that when the vortices are fixed the *total* force reacting on all the solid boundaries is given by

$$X = \sum_{i=1}^{n} \rho(\partial W/\partial x_i),\ Y = \sum_{i=1}^{n} \rho(\partial W/\partial y_i),$$

ρ being the density of the fluid. It can also be shown that ρW is a *measure* of the kinetic energy of fluid motion, so that equation (4.3) leads to the law of conservation of energy, W = constant.

[1] Kirchhoff, G., *Vorlesungen über mathematische Physik, Mechanik*, p. 255 ff. See also Lamb, H., *Hydrodynamics*, 1932, p. 230.

[2] Routh, E. J., *Proc. Lond. Math. Soc.*, **12**, 83 (1881).

[3] Even in the standard books of recent years, the treatment is far from complete; cf. Lamb, H., *Hydrodynamics*, 1932, pp. 219–236; Ramsey, A. S., *A Treatise of Hydro-*

mechanics, Pt. II, Hydrodynamics, 1935, pp. 219–232; Milne-Thomson, L. M., *Theoretical Hydrodynamics*, 1938, pp. 323–348.

[4] Lagally, M., *Math. Zeits.*, **10**, 231–239 (1921).

[5] Masotti, A., *Atti Pontif. Accad. Sci. Nuovi Lincei*, **84**, 209–216, 235–245, 464–467, 468–473, 623–631 (1931). Also, *Seminario Matematico e Fisico di Milano*, **6**, 3–53 (1932).

[6] The function called by Lagally the Kirchhoff's path function shall be called in this paper the "Kirchhoff-Routh function." The study of the function called by him the Routh's stream function is not of much importance, because it is merely a special application of the other (cf. equation (6.1)).

[7] For the definition of $O(\ )$ and $o(\ )$, cf. Titchmarsh, E. C., *Theory of Functions*, 1932, p. 1, Oxford.

[8] Koebe, P., *Acta Math.*, **41**, 306–344 (1918). Note that our function in case (*b*) is the function with two singularities, one at P_0, the other at infinity.

[9] Cf. Kellogg, O. D., *Foundations of Potential Theory*, 1929, pp. 238–240, Berlin. Note that no assumption is made regarding the nature of the boundaries $C_0, C_1, \ldots, C_k$.

ON THE MOTION OF VORTICES IN TWO DIMENSIONS—II SOME FURTHER INVESTIGATIONS ON THE KIRCHHOFF-ROUTH FUNCTION

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5. *Conformal Transformation.*—We shall now investigate the behavior of the Kirchhoff-Routh function (whose existence we have established in the preceding article) under a conformal transformation of fluid motion.

THEOREM II (*Generalized Routh's theorem*).—*Under a conformal transformation*

$$\tilde{z} = f(z) \tag{5.1}$$

which derives the motion in the $\tilde{z}$-plane from that in the z-plane, the Kirchhoff-Routh function for the new motion is given by

$$\tilde{W} = W + \sum_{i=1}^{n} \frac{\kappa_i^2}{4\pi} \log \left| \frac{dz}{d\tilde{z}} \right|_{P_i} \tag{5.2}$$

Proof. If $F(z)$ is the complex stream function in the z-plane, we have (*cf.*(2.3))

$$-u_i + iv_i = \lim_{P \to P_i} \frac{d}{dz} \left\{ F(z) - \frac{i\kappa_i}{2\pi} \log (z - z_i) \right\}. \tag{5.3}$$

We mark every quantity in the $\tilde{z}$-plane with a curl. The complex stream function for the new motion is then

$$\tilde{F}(\tilde{z}) = F(z), \tag{5.4}$$

by definition of conformal transformation. From this it follows that $\tilde{\kappa}_i = \kappa_i$, $(i = 1, 2, \ldots, n)$. It can be verified that, by (5.3) and (5.4),

$$-\tilde{u}_i + i\tilde{v}_i = (-u_i + iv_i)\frac{dz_i}{d\tilde{z}_i} + \frac{i\kappa_i}{4\pi}\frac{d}{d\tilde{z}_i}\log\left(\frac{dz_i}{d\tilde{z}_i}\right). \tag{5.5}$$

Multiplying (5.5) by δz_i and taking imaginary parts, we have

$$\tilde{v}_i\delta\tilde{x}_i - \tilde{u}_i\delta\tilde{y}_i = v_i\delta x_i - u_i\delta y_i + \frac{\kappa_i}{4\pi}\delta\log\left|\frac{dz}{d\tilde{z}}\right|_{P_i}. \tag{5.6}$$

Multiplying (5.6) by κ_i and summing for the index i, we have, by (4.3),

$$\delta\tilde{W} = \delta W + \delta\sum_{i=1}^{n}\frac{\kappa_i^2}{4\pi}\log\left|\frac{dz}{d\tilde{z}}\right|_{P_i}. \tag{5.7}$$

Equation (5.2) then follows at once (up to an additive constant).

6. *Discussion.*—(i) The above results hold when the solid boundaries are moving, for this affects the stream function ψ_0 alone. The Green function G, of course, depends upon the instantaneous configuration of the solid boundaries. Furthermore, the results hold also when the function ψ_0 has *fixed* singularities.

(ii) The theory gives explicitly the Kirchhoff-Routh function W by the formula (4.4) when the ordinary stream function (4.2) is known, for the functions ψ_0, G and g can then be written down at once. In actual applications, we must be careful to see that ψ is actually in the form (4.2), with ψ_0 and G satisfying required conditions.

(iii) *Routh's stream function and Routh's stream.*—By (4.3), the motion of the ith vortex may be derived from a *Routh's theorem function*

$$\chi_{(i)} = \frac{W}{\kappa_i} \tag{6.1}$$

by the formulas

$$u_i = -\frac{\partial\chi_{(i)}}{\partial y_i}, \quad v_i = \frac{\partial\chi_{(i)}}{\partial x_i}, \tag{6.2}$$

just as the fluid velocity is derived from the ordinary stream function ψ. By (4.4) and (5.2), we see that

$$\chi_{(i)} = \psi_0(x_i, y_i) + \sum_{j\neq i}\kappa_j G(x_i, y_i;\ x_j, y_j) + \frac{\kappa_i}{2}g(x_i, y_i;\ x_i, y_i) + h_i, \tag{6.3}$$

and transforms according to the law

$$\chi_{(i)} = \chi_{(i)} + \frac{\kappa_i}{4\pi}\log\left|\frac{dz}{d\tilde{z}}\right|_{P_i} + k_i, \tag{6.4}$$

under the transformation (5.1). In these equations, h_i and k_i are independent of x_i and y_i, and are therefore unimportant so far as the motion of the ith vortex is concerned. Equation (6.4) is *Routh's theorem* generalized to the case of a number of vortices.

Routh's original special case.—For a single vortex κ_0 at the point $P_0(x_0, y_0)$, the equations corresponding to (6.3) and (6.4) are

$$\chi = \frac{W}{\kappa_0} = \psi_0(x_0, y_0) + \frac{\kappa_0}{2} g(x_0, y_0; x_0, y_0) \tag{6.5}$$

and

$$\tilde{\chi} = \chi + \frac{\kappa_0}{4\pi} \log \left| \frac{dz}{d\bar{z}} \right|_{P_0}. \tag{6.6}$$

Equation (6.6) is *Routh's theorem* in its original form. In this case, the path of the vortex is given by

$$\chi = \text{const.}, \tag{6.7}$$

if the boundaries are fixed.

(iv) *Kirchhoff's original special case.*—If all the solid boundaries are absent, we have $g \equiv 0$. If, furthermore, there is no motion beyond that *due* to the vortices themselves, (4.4) reduces to the simple result

$$W = \frac{1}{2\pi} \sum_{\substack{i,j=1 \\ (i>j)}}^{n} \kappa_i \kappa_j \log r_{ij}, \quad r_{ij} = \sqrt{(x_i - x_j)^2 + (y_i - y_j)^2}, \tag{6.8}$$

first derived directly by Kirchhoff.[1]

In conclusion, the author wishes to express his sincere thanks to Prof. J. L. Synge, for suggesting the problem treated in these two articles and for his help and encouragement throughout the work. The author is also indebted to Dr. A. Weinstein for his kind help.

[1] Kirchhoff, G., *Vorlesungen über Mathematische Physik, Mechanik*, p. 225 ff. See also Lamb, H., *Hydrodynamics*, 1932, p. 230.

CONCERNING THE DIFFERENTIAL EQUATIONS OF SOME BOUNDARY LAYER PROBLEMS

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I. Mathematically the simplest boundary layer is that forming around a half-plane $y = 0$, $x \geqq 0$ immersed in an incompressible viscous fluid of kinematic viscosity ϵ^2 which flows by with a given constant velocity V in the direction of the x-axis. This two-dimensional steady flow can be described by a stream function $\psi^*(\epsilon;\ x, y)$, and if the viscosity ϵ^2 approaches zero, $\frac{1}{\epsilon}.\psi^*(\epsilon;\ x, \epsilon y)$ will tend to a limit $\psi(x, y)$, the stream function of the boundary layer. In our case ψ is of the form $2x^{1/2}.w(y/2x^{1/2})$ where the function w of the single variable $z = y/2x^{1/2}$ satisfies the non-linear differential equation

$$w''' + 2ww'' = 0 \quad (0 \leqq z < \infty). \tag{1}$$

One has to find a solution w for which $w = w' = 0$ at $z = 0$ and w' approaches V with $z \to \infty$. If $w(z)$ is a solution, so is $\beta.w(\beta z)$ whatever the positive constant β. Let $w = f(z)$ be the solution determined by the initial values $f = f' = 0$, $f'' = 1$. Once we are sure that f' tends to a positive limit a with $z \to \infty$,

$$a = \int_0^\infty f''(z)dz > 0, \tag{2}$$

we may adjust the constant β in such a way,

$$\beta^2 a = V, \tag{3}$$

that the derivative of $w = \beta.f(\beta z)$ approaches V at infinity.

When H Blasius carried out the integration as a first example of Prandtl's idea of the boundary layer,[1] he made use of the power series for w around $z = 0$ and of a certain asymptotic expression for large values of z, adjusting the constant β so as to make both expressions dovetail in a middle region. It is a fact, although it seems to have escaped notice, that convergence of the power series of f stops somewhere between $z = \sqrt[3]{9} = 2.08$ and $\sqrt[3]{30} = 3.11$. Thus Blasius' method, which has been followed later in many similar cases, can yield results of limited accuracy only, and the mathematician remains in doubt whether the solution f extends over the whole interval $z \geqq 0$ and has the property (2). After rejecting the power series because of its shortcoming, I shall here describe a rapidly converging process of successive and alternating approximations which gives all one may desire and is an excellent tool for actual numerical computation.

The coefficients c_n of

$$f(z) = \Sigma(-1)^n c_n z^{3n+2} \quad (n = 0, 1, \ldots)$$

are determined by the recursive formula

$$(3n + 2)(3n + 1)3n.c_n = 2.\Sigma(3i + 2)(3i + 1)c_i c_k \quad (i + k = n - 1)$$

and $c_0 = 1/2$. Notice that

$$\Sigma_0^{n-1}(3i + 2)(3i + 1) = n(3n^2 - 1)$$

and

$$1/30 \leqq \frac{3n^2 - 1}{3(3n + 2)(3n + 1)} \leqq 1/9 \quad (n = 1, 2, \ldots).$$

Hence the inequalities

$$c_i \leqq \frac{1}{2}\left(\frac{1}{9}\right)^i \text{ and } c_i \geqq \frac{1}{2}\left(\frac{1}{30}\right)^i$$

for $i = 0, \ldots, n - 1$ imply the same for $i = n$. Since they hold for $i = 0$ our statement is proved in the sharp form

$$\frac{1}{2}\left(\frac{1}{30}\right)^n \leqq c_n \leqq \frac{1}{2}\left(\frac{1}{9}\right)^n.$$

As is easily seen, the differential equation $f''' + 2ff'' = 0$ together with the initial conditions $f = f' = 0, f'' = 1$ is equivalent to the following integral equation for $g(z) = f''(z)$:

$$g(z) = \exp(-\int_0^z (z - \zeta)^2 g(\zeta) d\zeta) \quad \text{or} \quad g = \Phi\{g\}$$

where the functional operator Φ at the right side has the properties:

$$\Phi\{g\} \geqq 0, \Phi\{g\} \geqq \Phi\{g^*\} \text{ if } g \leqq g^*.$$

Thus we are led to define the successive approximations g_n by

$$g_{n+1} = \Phi\{g_n\} \quad (n = 0, 1, \ldots),$$

starting with $g_0(z) = 0$. The trivial relations $g_1 \geqq g_0 = 0, g_2 \geqq g_0 = 0$ then give rise to two sequences of inequalities:

$$g_0 \leqq g_1, g_1 \geqq g_2, g_2 \leqq g_3, g_3 \geqq g_4, \ldots$$

and

$$g_0 \leqq g_2, g_1 \geqq g_3, g_2 \leqq g_4, g_3 \geqq g_5, \ldots .$$

Hence the g_n perform an alternating pincer movement: all the odd g_n are

above the even g_n, the odd g_n move down, the even g_n go up with increasing n. Moreover one readily finds by induction with respect to n:

$$0 \leqq (-1)^n(g_{n+1}(z) - g_n(z)) \leqq \frac{(2z^3)^n}{(3n)!}.$$

Thus in the limit for $n \to \infty$ a solution g results which is approached by the even g_n from below, by the odd g_n from above.

The first approximations are

$$g_0 = 0,\ g_1 = 1,\ g_2 = e^{-1/3 z^3},$$
$$g_3(z) = \exp(-\int_0^z (z - \zeta)^2 . e^{-1/3 \zeta^3} d\zeta).$$

For large values of z the exponent in g_3 behaves like a quadratic polynomial,

$$\int_0^z (z - \zeta)^2 e^{-1/3 \zeta^3} d\zeta \sim a_2 z^2 - 2a'_2 z + a''_2$$

where

$$(a_2, a'_2, a''_2) = \int_0^\infty (1, \zeta, \zeta^2) . e^{-1/3 \zeta^3} d\zeta$$

and since $g \leqq g_3$ we have

$$g(z) \leqq e^{-kz^2}$$

for sufficiently high z if k is any positive number

$$< a_2 = \int_0^\infty e^{-1/3 \zeta^3} d\zeta = \sqrt[3]{3} . \Gamma\left(\frac{4}{3}\right).$$

This assures the convergence of

$$\int_0^\infty g(z) dz = \int_0^\infty f''(z) dz = a,$$

and the asymptotic behavior of

$$f(z) = \int_0^z (z - \zeta) g(\zeta) d\zeta$$

is indicated by

$$f(z) \sim \int_0^\infty (z - \zeta) g(\zeta) d\zeta = az - a'.$$

As $g \geqq g_2$ implies $a \geqq a_2$ we find the numerical coefficient $\alpha = a^{-1/2}$ in

$$w''(0) = \beta^3 = \alpha V^{1/2}$$

to be $< \alpha_2 = 0.684$. According to S. Goldstein,[2] $\alpha = 0.664$. Hence the very first approximate value for α which can be derived from our method misses the mark by less than 3%, which makes it likely that $g_3(z)$ is a pretty good approximation of $g(z)$ throughout the entire interval.

II. With slight alterations our process applies to the equation

$$w''' + 2ww'' - w'^2 = 0 \qquad (4)$$

which determines the wake behind our flat plate.[3] [The stream function of problem I for large $x \sim l$ assumes a finite value $\varphi(\eta) = \frac{\alpha}{4} V^{3/2}.\eta^2$ in the limit $l \to \infty$ after we make the substitution $y = \eta.l^{1/4}$, which we combine with $x - l = \xi.l^{1/4}$. With the plate ending at the point $x = l$, the stream function

$$\psi(\xi, \eta) = 3\xi^{3/2}.w(\eta/\xi^{1/2}) \quad (\xi \geqq 0)$$

of the wake is determined under the (not too good) assumption that it ties up with $\varphi(\eta)$ for $\eta/\xi^{1/2} \to \infty$.] The boundary conditions are:

$$w = w'' = 0 \text{ at } z = 0 \text{ and } w'' \to \tfrac{\alpha}{6}.V^{3/2} \text{ for } z \to \infty.$$

Let f be the solution with the initial values $f = 0, f' = 1, f'' = 0$. After differentiating (4),

$$f'''' + 2ff''' = 0, \tag{5}$$

we arrive at the following integral equation for $f'' = g$:

$$g(z) = \int_0^z \exp(-z^2 - \int_0^z (z - \zeta)^2 g(\zeta) d\zeta).dz.$$

$g(\infty)$ has a finite positive value, and thus one may adjust the constant δ in the solution $w = \delta.f(\delta z)$ so as to give to $w''(\infty)$ the desired value.

Neither of the equations (1) and (4) contains the independent variable z, and both allow the group of transformations $w(z) \to \beta.w(\beta z)$. Hence, as J. v. Neumann has observed, they are reducible to differential equations of the first order followed by two quadratures. They are thus within reach of Poincaré's general discussion of first-order differential equations. However, it seems certain that our method gives quicker numerical results and, what is more important, it works also in cases of a different type where that reduction is impossible.

III. One such case is the three-dimensional problem of a horizontal flow against a perpendicular wall.[4] Its differential equation

$$w''' + 2ww'' + (V^2 - w'^2) = 0 \tag{6}$$

holds for any value of the viscosity ϵ^2 and not merely in the limit $\epsilon \to 0$. Add the intial conditions $w = w' = 0$ at $z = 0$ and $w' \to V$ for $z \to \infty$. We try to construct a solution f of the equation (5) obtained by differentiation, for which $f = f' = 0, f'' = 1$ for $z = 0$ and the initial value $-a^2$ of f''' is such that f' approaches a finite limit for $z \to \infty$ (which then must equal a). The function $w = \beta.f(\beta z)$ solves our problem if β is chosen by (3). The integral equation for $f'' = g$ now reads

$$g(z) = a^2.\int_z^\infty e^{-\gamma(\zeta)} d\zeta$$

where

$$\gamma(z) = \int_0^z (z - \zeta)^2 g(\zeta) d\zeta, \; a^2 = 1/\int_0^\infty e^{-\gamma(\zeta)} d\zeta.$$

This time we have to start with $g_0(z) = 1$ and to construct the successive approximations by means of the formulas

$$\gamma_n(z) = \int_0^z (z - \zeta)^2 g_n(\zeta) d\zeta,$$
$$g_{n+1}(z) = \int_z^\infty e^{-\gamma_n(\zeta)} d\zeta / \int_0^\infty e^{-\gamma_n(\zeta)} d\zeta.$$

Readily enough, though by a somewhat more intricate argument, one establishes the alternating pincer movement of the sequence g_n. The question of convergence is of a different character and only convergence of the type of a geometric series is to be expected, because we are now dealing with a real boundary rather than an initial-value problem. I obtain majorizing constants μ_n,

$$0 \leqq (-1)^n (g_n(z) - g_{n-1}(z)) \leqq \mu_n,$$

defined by the recursive equations

$$\mu_1 = 1; \; \mu_n = q_n \cdot \mu_{n-1}, \quad \mu_{n+1} = q_n \cdot \mu_n \quad (n \text{ even})$$

where q_n denotes the constant

$$q_n = \int_0^\infty e^{-\gamma_{n-1}(\zeta)} \cdot \tfrac{1}{3!} \zeta^3 d\zeta / \int_0^\infty e^{-\gamma_{n-1}(\zeta)} d\zeta$$
$$= \int_0^\infty g_n(z) \cdot z^2 dz.$$

The second expression shows the alternating pincer movement of the q_n, hence all even $q_n \leqq q_2 = q$. If $q < 1$ our process converges uniformly and better than the geometric series of quotient q. Since $q_1 = 1/3$ our experience with problem I leads us to expect that q is not much larger than $1/3$; a provisional calculation indicates that its value is about 0.41.

Queerly enough, the differential equation of the corresponding two-dimensional problem, first treated by Hiemenz,[5]

$$w''' + 2ww'' + 2(V^2 - w'^2) = 0, \tag{7}$$

proves less tractable, not so much for want of an appropriate recursive process—which can be set up after twice differentiating (7)—as for want of a proper start $g_0(z)$.

The boundary layer of the two-dimensional flow against an angular bastion of angle $\pi\lambda$ may be determined by conformally mapping the exterior of the angle upon an $(x + iy)$-plane cut along the positive x-axis. Introducing Prandtl's coördinate $y^2/2x^{1/2}$ in that plane, one obtains the differential equation

$$w''' + 2ww'' + 2\lambda(V^2 - w'^2) = 0.$$

Hence the rectangular bastion, $\lambda = 1/2$, leads to Homann's equation (6) which showed itself accessible to our method. I do not know how to deal with values of the constant λ other than $\lambda = 0$ and $1/2$.

I wish the WPA Mathematical Tables Project could be persuaded to resume computation of tables for the functions f, f', f'' of the problems I, II, III by the systematic procedure here explained.

[1] *Zeitschr. Math. Phys.*, **56**, 1 (1908).

[2] *Proc. Cam. Phil. Soc.*, **26**, 1–30, especially p. 19 (1930). See also Howarth, L., *Proc. Roy. Soc.*, **164A**, 551 (1938), and Goldstein, S., *Modern Developments in Fluid Dynamics*, Oxford, 1938, p. 136.

[3] Goldstein, S., loc. cit.,[2] and *Proc. Roy. Soc.*, **142A**, 545–573 (1933).

[4] Homann, F., *Zeitschr. angew. Math. Mech.*, **16**, 153 (1936).

[5] *Dingler's Polytech. Jour.*, **326**, 321–326 (1911).

THE GENERATION OF INSEPARABLE FIELDS

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1. Introduction.—The chief difficulties with fields of characteristic p arise in treating inseparable extensions; that is, extensions defined by irreducible polynomials with multiple zeros. Such extensions occur in various arithmetic questions; for instance, in the treatment of the residue class fields of certain complete topological fields. This leads to the study of ways of generating these extensions so as to minimize inseparability.

To generate an extension K of a field k of characteristic p, first pick a transcendence basis T: the elements of T are algebraically independent over k, and every element of K is algebraic over the field $k(T)$ generated by adjunction of all elements of T. In case every element of K satisfies a separable algebraic equation over $k(T)$, we say that T is a *separating transcendence basis*. Such a basis does not always exist[1] for given K and k. But for any T, Steinitz[2] showed that the sets

$$S_n = \{\text{all } u \in K \text{ with } u^{p^n} \text{ separable over } k(T)\} \qquad (1)$$

are subfields of K, and that every element of K is in one of these subfields. Thus K is the "limit" of a tower of fields

$$k \subset S_0 \subset S_1 \subset S_2 \subset \ldots \text{ (for given } T). \qquad (2)$$

If each field S_n of this tower has an individual separating transcendence basis T_n over k, we say that the tower[1] belonging to T can be *separated*.

If k and K are both perfect fields, every tower can be separated. Our main theorems state conditions under which towers for *imperfect* fields can be separated.

These conditions involve properties of p-independence. A set of elements of k is said to be *p-independent*[3] in k if no one of the elements lies in the field generated by the remaining elements and all pth powers from k. A particularly simple class of extensions are those extensions K/k which *preserve p-independence*,[1] in the sense that every subset of k p-independent in k remains so in K. If the base field k is perfect, none of its subsets are p-independent and every extension preserves p-independence.

2. Denumerable Field Towers.—Throughout this section we consider an extension K/k which preserves p-independence and which has a finite or denumerable transcendence basis over k.

THEOREM 1. *The Steinitz tower (2) for K/k can be separated relative to a suitably chosen transcendence basis T.*

One of us previously published without proof a similar theorem,[4] asserted for all choices of transcendence basis. Subsequent examples showed that this formulation needed to be modified. A reëxamination of the original unpublished proof then easily gave a proof of this theorem above, for a *suitable* choice of the transcendence basis T. The essential point in the proof of this theorem is the idea of replacing the original denumerable transcendence basis $t_0, t_1, t_2, \ldots$ by a new basis $t_0, t_1^p, t_2^{p^2}, \ldots$. For every integer n, all but a finite number of elements of this new basis are p^nth powers in the field K. This property means that the difficulties involve only a finite number of transcendentals, which can then be treated as in the special case[5] of this theorem in which the transcendence basis is finite.

In the proof, the transcendence basis T_n already given for a field S_n of the tower is first changed so that as many elements as possible are pth powers. Let $T_n^{[p^{-1}]}$ be the set obtained from T_n as follows: if $t \in T_n$ has a pth root u in K, replace t by u; if not, replace t by t. This will give a separating basis for S_{n+1}, as follows.

THEOREM 2. *In Theorem 1 the separating transcendence basis T_n for the extension S_n/k may be so chosen that the set $T_n^{[p^{-1}]}$ is a separating transcendence basis for S_{n+1} over k.*

The hypothesis that K/k preserve p-independence is necessary for the validity of Theorem 1. It is used to show that certain irreducible equations in n parameters contain[6] terms which are not pth powers. The proof also gives the

COROLLARY. *If K/k has a finite transcendence basis, every tower (2) can be separated.*

For the arithmetic applications it is desirable to have a tower with a number of more specific properties, as follows.

THEOREM 3. *K is the limit of a tower*

$$k \subset L \subset M_0 \subset M_1 \subset M_2 \subset \ldots \tag{3}$$

with the following properties: (*i*) *K can be generated by elements of L and by* pth *powers from K.* (*ii*) *L has a separating transcendence basis over k.* (*iii*) *K/L preserves p-independence, and L is algebraically closed in K.* (*iv*) *Each* M_n *is algebraic over* M_{n-1}. (*v*) *Each* M_n *has a separating transcendence basis over L.* (*vi*) *Each* M_n *can be generated from L by the adjunction of* pth *powers of elements which lie in* M_{n+1} *but not in* M_n.

The last property stated in this theorem is the essential one for the applications.[7] For the proof, the field L is first constructed by adjoining to k a relative p-basis of K and taking the algebraic closure of this field. The requisite fields M are then found by making a selection from the fields of a Steinitz tower for K over L, using the results of Theorem 2.

3. *General Field Towers.*—The analysis of extensions with a non-denumerable transcendence basis depends on the following result.

THEOREM 4. *If an extension K preserves p-independence over k, then K can be represented as the limit of a* (*transfinite*) *tower of fields*

$$K_0 = k \subset K_1 \subset K_2 \subset \ldots \subset K_\alpha \subset K_{\alpha+1} \subset \ldots \subset K \tag{4}$$

in which each $K_{\alpha+1}$ *preserves p-independence over* K_α *and can be generated from* K_α *by a denumerable set of elements. Furthermore, if the index* β *is a limit number, the corresponding field* K_β *is the union* (*the limit*) *of all the fields* K_α *with indices* $\alpha < \beta$.

The proof is obtained by building up $K_{\alpha+1}$ by adjoining to K_α any specified element of $\bar{K}$, followed by a denumerable sequence of adjunctions sufficient to realize in $K_{\alpha+1}$ any relations of p-independence which may hold in the whole field K.

4. *Arithmetic Applications.*—The original investigations[4] of the Steinitz towers (2) were intended to yield a proof of the structure theorem for p-adic fields, which asserts that a p-adic field $\mathfrak{K}$ is uniquely determined[8] up to isomorphism, by its field K of residue classes. The revised form of the Steinitz tower theorem (Theorems 3 and 4) is adequate to carry through the original proof of this structure theorem. Specifically, let the given p-adic field $\mathfrak{K}$ have a residue class field K, of characteristic p. Then K preserves p-independence over its prime field k. Parallel to the transfinite tower (4) of extensions preserving p-independence one can construct[9] a tower of p-adic fields.

$$k = \mathfrak{K}_0 \subset \mathfrak{K}_1 \subset \mathfrak{K}_2 \subset \ldots \subset \mathfrak{K}_\alpha \subset \mathfrak{K}_{\alpha+1} \subset \ldots \subset \mathfrak{K}'. \tag{5}$$

To prove the structure theorem it suffices to show that the given field $\mathfrak{K}$ is isomorphic to the constructed p-adic field $\mathfrak{K}'$, under a correspondence ϕ

which induces the identical isomorphism on the residue class fields. This ϕ can be built up by steps according to the steps given in (5). If ϕ_α is a given isomorphism of the field $\mathfrak{K}_\alpha$ into a subfield of $\mathfrak{K}$, an extension $\phi_{\alpha+1}$ of ϕ_α to $\mathfrak{K}_{\alpha+1}$ can be constructed as the limit of a sequence of correspondences belonging to a suitable tower of residue class fields for $K_{\alpha+1}$ over K_α. The special properties of this tower as given in Theorem 3 suffice to insure the convergence of this sequence, just as in the previous proof.[4] However, the use of the "grundring" in this proof is avoided by the preliminary construction (5) of a fixed tower of p-adic fields.

This step from K_α to $K_{\alpha+1}$ is actually a proof of a type of relative structure theorem, which asserts the extendability of an isomorphism between two p-adic fields to an isomorphism of two p-adic extensions with the same (denumerable) residue class extension, provided the latter extension preserves p-independence.

5. Extensions Preserving p-Independence.—The extensions of this type, which are requisite for the above proof, may be described in various fashions. A field k of characteristic p may be called *inseparably* (or separably) *algebraically closed* in an extension K if no element of the complement $K - k$ is inseparable (or, separable) and algebraic over k. Also k is *strongly inseparably* (separably) *algebraically closed* in K if every finite extension k^* of k is inseparably (separably) closed in every one of the composites k^*K. These concepts are refinements of the notion of strong algebraic closure ("streng transcendenz") introduced by Krull in some ideal theoretic investigations.[10] One has

THEOREM 5. *An extension K over a field k of characteristic p preserves p-independence if and only if k is strongly inseparably algebraically closed in K.*

The proof uses the following extension of a Lemma by Krull.

LEMMA. For given $K \supset k$, let k^{**} be the maximum subfield algebraic over k in a composite k^*K of K with a finite extension k^* of k. If k is separably (inseparably) algebraically closed in K, then the reduced degrees (the exponents) of k^*/k and k^{**}/k are the same.

There are also the following characterizations of extensions preserving p-independence.

THEOREM 6. *Let T be a transcendence basis for K over k. Then K preserves p-independence over k if and only if the algebraic extension $K/k(T)$ is not reduced by $k^{p^{-1}}(T)$.*

If the property stated here holds for one T, it holds for every T. To say that $K/k(T)$ is "reduced" by $k^{p^{-1}}(T)$ means that there is a finite extension L generated from $k(T)$ by pth roots of elements from k such that the degree

$$[KL : K] < [L : k(T)].$$

THEOREM 7. *The extension K/k preserves p-independence if and only if every transcendence basis T for K/k has the following property: for every*

polynomial $f(x^p, T)$ irreducible in $k[x, T]$ with a root $x = \alpha$ in K there is at least one element of T which appears once in f with an exponent not divisible by p.

* The results of this paper were originally intended for publication in full in a German mathematical periodical. This plan has been interrupted by circumstances beyond our control. The present summary was prepared by the younger of the authors, so that the senior author bears no responsibility for the present form of the results.

[1] MacLane, S., "Modular Fields I, Separating Transcendence Bases," *Duke Math. Jour.*, **5**, 372–393 (1939). Definitions of the various terms used for modular fields may be found here, or in the book[2] by Steinitz.

[2] Steinitz, E., *Algebraische Theorie der Körper*, edited by R. Baer and H. Hasse, Berlin, 1930.

[3] Teichmüller, O., "p-Algebren," *Deutsche Mathematik*, **1**, 362–388 (1936).

[4] Hasse, H., and Schmidt, F. K., "Die Struktur discret bewerteter Körper," *Jour. reine angewandte Math.*, **170**, 4–63 (1934).

[5] MacLane, S., "Steinitz Field Towers for Modular Fields," *Trans. Am. Math. Soc.*, **46**, 23–45 (1939).

[6] The exact property used is that stated in Lemma 2 of the paper of footnote 1.

[7] See the discussion in 5, §§ 5 and 9.

[8] See the detailed discussion of structure theorems in MacLane, S., "Subfields and Automorphism Groups of p-Adic Fields," *Ann. Math.*, **40**, 423–442 (1939).

[9] By the extension theorem (Theorem 2) stated in the article 8.

[10] Krull, W., "Beiträge zur Arithmetik kommutativer Integritätsbereiche VII, Inseparable Grundkörpererweiterung. Bemerkung zur Körpertheorie," *Math. Zeit.*, **45**, 319–344 (1939).

MAXIMAL INVARIANT PROPER SUBGROUPS OF A FINITE GROUP

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In order to avoid misunderstanding it should be emphasized that a maximal invariant proper subgroup of a given group G is not necessarily a maximal proper subgroup of G although it might at first appear that the latter should include the former and that the term invariant should refer to a subdivision of maximal proper subgroups. The commonly used definitions of these terms are that a maximal invariant proper subgroup is an invariant proper subgroup which does not appear in a larger invariant proper subgroup of the group, while a maximal proper subgroup is a proper subgroup which is not found in a larger proper subgroup of the group. A necessary and sufficient condition that a maximal invariant proper sub-

group of a group is also a maximal proper subgroup of the group is therefore that the corresponding quotient group of the former is of prime order.

There is a well-known group of order 120 which contains only one invariant proper subgroup and this is of order 2. The corresponding quotient group is therefore of composite order and hence this maximal invariant proper subgroup of the group is not a maximal proper subgroup of it. Some writers include the subgroup formed by the identity among the proper subgroups of a group while the majority seem to exclude the identity from the proper subgroups. We follow the latter custom and call the identity and the group itself trivial subgroups. The custom of including the group itself among its subgroups is widely followed although this is not universal. In such cases we aim to follow the most common usage irrespective of personal preferences based on inconclusive evidence. Unfortunately there are still many terms in the group theory literature, including the term group itself, which are being employed with widely different meanings, but the context usually exhibits the intended meaning.

Both the maximal invariant proper subgroups and the maximal proper subgroups were introduced into group theory on account of their applications in the theory of equations. The former were introduced by C. Jordan (1838–1922) who proved the constancy of the factors of composition of a group, while the latter were emphasized by W. Dyck (1856–1934) who proved that a necessary and sufficient condition that a transitive permutation group is primitive is that its subgroup composed of all its permutations which omit a given letter is a maximal subgroup of the group. When all the maximal subgroups of a group are also invariant subgroups of the group then the group is the direct product of its Sylow subgroups and vice versa. It has recently been proved that when all the maximal proper subgroups of a group are of the same order then the group is a prime power group and vice versa (see these PROCEEDINGS, **27**, 445-448 (1941)).

Suppose that no two of the maximal proper subgroups of the group G are of the same order. Every maximal proper subgroup of G is therefore invariant under G since conjugate subgroups have the same order, and hence G is the direct product of its Sylow subgroups. Moreover, each of these Sylow subgroups is cyclic and no two of them can have the same order. Hence it results that *a necessary and sufficient condition that no two of the maximal proper subgroups of a given group are of the same order is that the group is the direct product of prime power cyclic groups such that no two of these groups have orders which are powers of the same prime number.* In particular, all such groups are cyclic and vice versa. The two extreme cases when every two maximal proper subgroups of a group are of the same order and when every two of the maximal proper subgroups of a group are of different orders therefore relate to very elementary categories of groups.

The former condition is a characteristic property of prime power groups while the latter is a characteristic property of cyclic groups.

A complete set of conjugate maximal proper subgroups of a group is transformed under the group according to a non-regular primitive permutation group since one of these maximal proper subgroups cannot transform another into itself because the two generate the entire group. Hence the permutation group according to which they are transformed under the group is not only primitive but also non-regular. Therefore it results that when a group does not contain more than two maximal proper subgroups of the same order then all of its maximal proper subgroups are invariant and the group is the direct product of its Sylow subgroups. As such a group could not involve exactly two maximal proper subgroups of the same order the entire group could not involve exactly two maximal proper subgroups of the same order. That is, *if a group contains at most two maximal proper subgroups of the same order every two of its maximal proper subgroups are of different orders and hence it is cyclic.*

In a solvable group the number of subgroups in a complete set of conjugate maximal proper subgroups is a power of a prime number since such a set is transformed under these subgroups according to a non-regular primitive permutation group which is solvable. Every non-regular primitive permutation group of degree n is the group of transformation of maximal proper subgroups since it transforms its n subgroups of degree $n - 1$, composed separately of all its permutations which omit a given letter, in the same way as it transforms its own letters. On the contrary, an imprimitive permutation group cannot transform a set of conjugate maximal subgroups in the same way as it transforms its own letters because the subgroup formed by all its permutations which omit one letter cannot be maximal. It may be noted that when a group contains only one maximal proper subgroup it follows from the given general theorems that it must be a prime power group because all its maximal proper subgroups are of the same order and it must be cyclic because all of its maximal proper subgroups are of different orders. Hence it must be a cyclic prime power group, as is also otherwise evident.

We add as a matter of independent interest that the term abelian group is widely used in the recent literature of group theory but writers who desire to refer to its origin are apt to be perplexed by the apparently conflicting statements found in places where they are likely to look first. For instance, in the second edition, volume 1, "Enzyklopädie der Mathematischen Wissenschaften," page 6, 9 (1939), there appears a note stating that L. Kronecker speaks of abelian equations, and H. Weber of abelian groups in the first edition of volume 1, page 536, of his algebra. As the date of this algebra is 1895 one might at first be inclined to think that the term abelian group was adopted comparatively recently. In the "Encylopédie

des Sciences Mathématiques," tome 1, volume 1, page 601, it is added that J. Perott used the term sulerien groups for abelian groups in *American Journal of Mathematics*, **11**, 99 (1889).

This matter is somewhat complicated by the fact that C. Jordan used the term abelian group, with a somewhat different meaning from that now commonly assigned to it, in his widely used "Traité des substitutions" (1870), and a little earlier, in *Mathematische Annalen*, **1**, 584 (1869). It may therefore be of interest to note here that H. Weber used this term with its modern common meaning in *Mathematische Annalen*, 20, 304 (1882). The great influence of H. Weber in the early developement of group theory naturally led to the rapid adoption of this term with its present most commonly accepted meaning notwithstanding the great influence of Jordan's "Traité."

RADIOACTIVE CARBON AS AN INDICATOR OF CARBON DIOXIDE UTILIZATION. VII. THE ASSIMILATION OF CARBON DIOXIDE BY MOLDS

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The application of labeled carbon to the study of the metabolism of various biological systems has indicated that CO_2 may play an important rôle in intermediary metabolism. Among the numerous heterotrophic, non-photosynthetic systems already studied in this connection are yeast,[1] Lebedev juice,[2] various bacteria,[1-5, 15] plant (root)[1,6] and animal tissues.[1, 9, 10, 11]

The fungi comprise a large and important group of non-chlorophyllous heterotrophic organisms. Carbon dioxide assimilation by these organisms had never been investigated because they normally produce such vast quantities of CO_2 that it would be impossible to detect CO_2 assimilation by ordinary chemical methods. Since the use of labeled carbon has yielded valuable information concerning CO_2 utilization it was of great interest to extend the radioactive carbon studies to an investigation of mold metabolism.

For a study of CO_2 utilization by molds, we used strains whose general metabolic characteristics had been studied previously.[12, 13, 14] These molds were:

(1) A strain of *Rhizopus nigricans* which forms large quantities of fu-

maric acid from glucose. The fumaric acid production was of special interest in view of the fact that the very closely related compound, succinic acid, is known to be formed in part from CO_2 by bacteria.[3, 6, 7]

(2) A *Rhizopus* species which is characterized by its ability to produce lactic acid from glucose. A study of this mold was of interest since the lactic acid produced by bacteria (*Streptococcus lactis*) in the presence of C^*O_2 was not radioactive.[2]

(3) A strain of *Aspergillus niger* which is known to produce large amounts of citric acid from sugar. It has been suggested that the synthesis of citric acid by molds may involve a fixation of CO_2.[16] In order to ascertain whether or not this is true, it was only necessary to carry out experiments on citric acid production in the presence of C^*O_2.

Both *Rhizopus* species were grown in 5 per cent dextrose, 0.1 per cent $(NH_4)_2SO_4$, 0.05 per cent $MgSO_4$ and 0.02 per cent KH_2PO_4. The growth medium for *Aspergillus* was similar except that sucrose was used instead of dextrose, 2 ml. of yeast autolysate were added per liter of medium and the pH was adjusted to 3.0 with HCl.

Molds grown in stationary liquid cultures produce a thick pellicle on the surface of the medium. This type of growth is entirely unsuitable for use in metabolic studies on account of its physical and physiological inhomogeneity, as Kluyver and Perquin have ably demonstrated.[17, 18] Therefore the medium was inoculated with a spore suspension of the mold, and the flask was placed on a rotary shaking machine at 30°C. for one to two days. By this means a submerged type of growth is obtained, which represents a homogeneous suspension of mold material.[17, 18]

Experiments on Fumaric Acid Production by Rhizopus Nigricans.—Suspensions of the mold mycelia were placed in a 5 per cent glucose solution with C^*O_2 in the gas phase, and were shaken at 30°C. for 30 minutes in the presence and in the absence of O_2. Under the experimental conditions prevailing, the mold converted ~10 per cent of the available C^*O_2 into organic compounds. Table 1 contains a summary of the results.

TABLE 1

	AEROBIC[a] 30 MINUTES	ANAEROBIC[a] 30 MINUTES
Total C* in supernatant solution[d] after centrifuging off the cells	19.5	29.
Fumaric* acid[c] in this solution	8.	25.
C* in neutral volatile distillate	0.1	0.2
Total C* in acid extract[b] of cells	44.	30.
Fumaric* acid in this solution	6.5	12.
C* remaining in cells after acid extraction	36.5	41.

[a] These quantities are expressed as per cent of the total C^*O_2 assimilated.
[b] Prepared by gentle boiling with dilute fumaric acid solution.
[c] The fumaric acid was precipitated as mercurous fumarate.[19]
[d] Dissolved CO_2 removed before radioactivity measurements.

It appears that the fumarate produced anaerobically contains a greater fraction (37 per cent) of the C* assimilated than aerobically (14.5 per cent). It is of considerable interest to note that 36–40 per cent of the C* was converted into acid-insoluble cellular material. This cellular material, which remained after acid extraction, was divided into two portions and treated as follows:

(1) One fraction was boiled for one hour in 2 *N* HCl in order to hydrolyze insoluble polysaccharides. After filtration the soluble material was found to contain less than 0.6 per cent of the total C*.

(2) The second fraction was extracted for one hour with pentane in a Soxhlet extraction apparatus. The extract contained <0.1 per cent of the total C* assimilated.

These results show that the acid-insoluble radioactive material consists neither of easily hydrolyzable polysaccharide nor of fat. This is of interest because the fungi are known to form large quantities of such substances.

TABLE 2

FRACTION TESTED	C* CONTENT[a]
Aqueous acid extract of cells	30
Cells after acid extraction	69
Neutral volatile	1

[a] Expressed as per cent of assimilated C*.

The most interesting result of these experiments was the demonstration that C^*O_2 enters into the synthesis of the C_4 dicarboxylic acid, fumaric acid. This is of special significance in view of the fact that the closely related C_4 dicarboxylic acid, succinic acid, is synthesized in part from C^*O_2 by certain bacteria. Since the latter substance contains labeled carbon only in the carboxyl groups,[7] it was of interest to ascertain whether the fumaric acid produced by *Rhizopus nigricans* also contains C* in this position only.

The fumaric* acid was oxidized with $KMnO_4$ in 1.5 *N* H_2SO_4. Under these conditions one mole of fumaric acid yields 3 moles of CO_2 and 1 mole of formic acid. It was found that the CO_2 contained all the radioactivity of the original fumarate, whereas the formic acid was inactive. Since recent experiments[20] have clearly demonstrated that the formic acid is derived exclusively from the central carbon atoms of the fumaric acid, it is evident that the radioactive carbon in the fumarate was located in the carboxyl groups only.

Experiments on Lactic Acid Production by Rhizopus Sp.—A suspension of *Rhizopus* sp. was placed in a 5 per cent glucose solution, and allowed to metabolize aerobically in the presence of C^*O_2 at 30°C. for 30 minutes. The results obtained are summarized in Table 2.

The acid extract was obtained by gently boiling the suspension with di-

lute lactic acid solution. Insoluble cellular material was removed by centrifugation. The aqueous solution was exhaustively extracted with ether, after which the ether was found to contain 25 per cent of the C* present in the acid extract.

In another experiment the radioactive substances in the aqueous acid extract was partitioned between ethyl ether and water, lactic acid being added as carrier. The partition coefficients of the radioactivity obtained by successive extractions with ether were very different from those determined by titrimetric measurements on the carrier lactic acid. One may conclude, therefore, that lactic* acid could be present only in small amounts, if at all, and that the radioactivity was due mainly to other ether-soluble acids.

It is known that this strain of *Rhizopus* produces small amounts of fumaric acid in addition to lactic acid. In fact, the partition coefficients of the material, calculated from successive extractions of the aqueous solution with ether, were in rough agreement with those of fumaric acid determined under exactly the same conditions. The results are summarized in Table 3.

TABLE 3

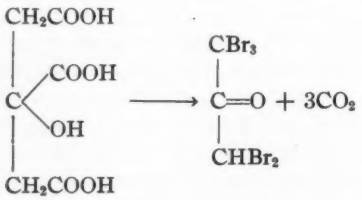
	PARTITION COEFFICIENTS	
	BY RADIOACTIVITY MEASUREMENTS	BY TITRATION FOR FUMARIC ACID
Fraction 1	1.34	1.49
Fraction 2	0.66	0.88
Fraction 3	0.91	1.09

It would appear as if an appreciable portion of the ether-extractable radioactive acids consists of fumaric* acid.

In order to definitely establish that fumaric* acid was produced by this mold an additional experiment was carried out in which the fumaric* acid was isolated and identified by precipitation with Hg_2^{++} in 5 per cent HNO_3.[19] This precipitate contained 13 per cent of the C* content of the acid extract, indicating that ~50 per cent of the ether-soluble radioactivity was due to fumaric* acid.

Experiments on Citric Acid Production by Aspergillus Niger.—The cell material was suspended and shaken in a 5 per cent sucrose solution in the presence of C^*O_2 and air for 40 minutes. The cells were then centrifuged off, and after removing residual C^*O_2 from the supernatant solution, citric acid was added as a carrier. The solution was made slightly alkaline and calcium citrate was precipitated by the addition of $CaCl_2$ to the boiling solution. The precipitate was collected by filtration, dissolved by the addition of HNO_3, and reprecipitated as before. This purification process was repeated once more. The precipitate was found to contain ~14 per cent of the C* originally present in the supernatant culture liquid, indicating that C^*O_2 had entered into the synthesis of citric acid.

An aliquot of the Ca citrate* was decarboxylated and converted into pentabromoacetone. The transformation can be represented as follows:



The decarboxylation was performed by adding KBr in 25% H_2SO_4 to the citric* acid solution and allowing the mixture to stand for 10 minutes at room temperature followed by 5 minutes at 50°C. An excess of 5 per cent $KMnO_4$ solution was then added. The liberated CO_2 was bubbled through a solution of $Ca(OH)_2$ and the radioactivity of the resultant $CaCO_3$ determined. The residual MnO_2 was reduced with 20 per cent $FeSO_4$, the solution cooled to 0°C., and the insoluble pentabromoacetone filtered off.

The CO_2, which is very likely derived from the three carboxyl groups, contained 50 times more C* than was found in the pentabromoacetone, indicating that the C* in the citric* acid was mainly, if not all, in the carboxyl groups.

The above experiments demonstrate that CO_2 does participate in the synthesis of citric acid by *A. niger*. Moreover, the degradation of the citric acid molecule indicates also in this case the C* is restricted to the carboxyl groups.

Discussion.—The experiments described in the present paper represent the first direct evidence that fungi assimilate CO_2. That CO_2 enters into the metabolism of fungi has been suggested by Rockwell and Highberger[21] who observed that the absence of CO_2 delayed the initiation of growth of various fungi. Golding[22] obtained similar results with strains of *Penicillium roquefortii*, and in addition found that increasing the CO_2 pressure, up to 20 per cent, had a distinct accelerative effect on growth. Higher partial pressures of CO_2 were repressive (see also Kuhn[23]). The experiments of Hes[24] indicated that CO_2 is necessary for the normal functioning of respiratory catalysts in *Aspergillus niger*, because methylene blue reduction was considerably slower in the absence of CO_2.

It is especially in the case of the molds that a large part of the C^*O_2 assimilated is retained as cellular substance; this is of interest since molds as a group are known to utilize sugar substrates with a high degree of efficiency in regard to the synthesis of cellular material. Although the results presented above are essentially qualitative due to technical difficulties (short half-life of C^{11}), they appear to indicate that the CO_2 utilization by molds

does not reach the magnitude attained by other systems, e.g., the propionic acid bacteria. Yet, CO_2 may be quantitatively quite significant in cellular synthesis by molds. The large proportion of assimilated C* found in the acid-insoluble cellular material strengthens this belief. Furthermore, it should be borne in mind that the experimental conditions were not conducive to maximum C^*O_2 utilization. This is shown by the following considerations: (1) Low partial pressures of C^*O_2 were used, and from the experiments of Golding[22] and others on the beneficial effects of high CO_2 tensions it seems reasonable that in the present experiments the rate of CO_2 uptake was below the maximum. (2) During the course of the experiment, the mold was producing large quantities of CO_2, due to the oxidation of the substrate, and thus the C^*O_2 was diluted to a considerable extent. (3) Mold cells are relatively large in volume, and a fair proportion of the respiratory CO_2 may be assimilated *in situ* before it has a chance to diffuse out.

It is apparent that once C^*O_2 has been assimilated by the molds, the C* containing compounds enter into many metabolic reactions as evidenced by the fact that C* was found in a variety of substances, namely, neutral volatile compounds, fumaric and citric acids, and soluble and insoluble cellular material consisting of as yet unidentified compounds. The finding of an appreciable portion of the C* in these substances is interesting since it shows that CO_2 enters into the main respiratory channels. One point of entry may be the formation of oxaloacetate* from pyruvate and C^*O_2, a reaction already suggested from studies with bacteria,[7, 6, 25] pigeon liver[26] and yeast.[27] The oxaloacetate* so formed could give rise to fumaric* acid by the same reactions described for the formation of succinic *[6, 7, 29] and form citric* acid by the reactions proposed by Krebs for the citric acid cycle.[28]

The production of citric acid in part from CO_2 is of interest in connection with some anomalous yields of this acid reported in the literature. It has been proposed[30] that prior to the formation of citric acid by fungi the sugar first undergoes a yeast-like fermentation to acetaldehyde which is then supposed to give rise to acetic acid, two molecules of which in turn condense to form a 4-carbon dicarboxylic acid. The latter can then condense with a third 2-carbon compound to produce the 6-carbon compound, citric acid. There is no experimental evidence for either of these condensation reactions; also, according to this theory the sugar could never yield more than 71 per cent citric acid (by weight) and the weight ratio of citrate/CO_2 formed should not exceed 1.45. There are a few instances[31] where significantly larger yields of citric acid have been reported. As much as a 90 per cent yield of citric acid has been found by Wells, *et al.*, accompanied by a proportionately high citrate/CO_2 ratio. These authors suggested that pyruvate arising during the breakdown of the sugar may have been utilized

directly for citrate synthesis without being decarboxylated to a 2-carbon compound + CO_2. In view of the results reported in the present paper, the possibility of CO_2 utilization in the synthesis of citric acid must be considered. It is conceivable that the well-known variations in citric acid producing capacity among strains of *Aspergilli* and *Penicillia* may be due in part to differences in capacity for utilizing CO_2.

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